ENVIRONMENTAL PHYSIOLOGY OF THE LITTLE PENGUIN

(Eudyptula minor)

by

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Declaration

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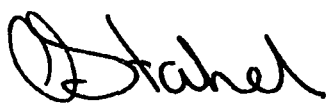

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ABSTRACT

This study investigates the energetic adaptations and constraints of the little penguin in relation to its aquatic lifestyle and examines the possible function of sleep as an energy conserving mechanism.

The little penguin had a similar level of standard metabolic rate to other birds. Body temperature was lower than the general avian level and varied with the site of measurement. Although penguins may be considered cold-adapted due to the thermal consequences of immersion; the results of this study and analysis of published data for other species shows minimal conductance in penguins appears to be relatively high in comparison to other cold-adapted birds due to the shallow insulative layer provided by the penguins waterproof plumage. This limitation is to some extent compensated by a well-developed capacity to alter body insulation. Water represents a severe thermal challenge to the little penguin since the potential for heat loss is two orders of magnitude greater than in air. Heat balance in water was maintained by prevention of excessive heat loss through insulative changes. Limits to the extent of insulation restrict the ability of the little penguin to withstand low water temperatures.

Respiratory ventilation in the little penguin was much less than expected due to a low respiratory frequency and conferred a very high oxygen extraction coefficient. Ventilation during cold exposure remained closely associated with metabolic demands. The high gas exchange efficiency in the little penguin correlates well with its short aerobic diving patterns. Heat exposure resulted in large increases in ventilation and the limited capacity of little penguins to withstand heat exposure is in part explained by low tolerance to changes in acid-base status.

The metabolic response to wind in the little penguin varied with temperature. At thermoneutrality increased convective heat loss with wind was compensated by an increase in body insulation. During cold

exposure body and plumage insulation had attained maximal values whereupon increased windspeed resulted in a linear increase in metabolic heat production. The dense, overlapping feathers of the little penguin, however, provide an effective resistance to increased heat loss associated with windspeed. The primary effect of wind upon partitional insulation at neutral and cold temperatures was a decrease in the insulation provided by the thermal boundary layer.

Little penguins showed similar electrophysiological correlates of sleep to other birds and exhibited polyphasic sleep patterns. This study showed that the amount of sleep increased at night due to increased frequency of sleep periods and decreased during cold exposure due to a reduction in the length of sleep periods. Sleep was associated with decreased metabolic rate compared to values in quiet wakefulness. This decrease, however, represented only a marginal reduction in daily energy costs.

INTRODUCTION

> "... the Penguins and Manchots appear to form the shade between birds and fish. Instead of wings they have little pinions, which might be said to be covered with scales rather than feathers, and which serve as fins; their body is large, compact, and cylindrical, behind which are attached two broad oars, rather than two legs: the impossibility of advancing far into the land, the fatigue even of remaining there, otherwise than by lying; the necessity, the habit of being almost always at sea, their whole economy of life, mark the analogy between the aquatic animals and these shapeless birds, strangers to the regions of air, and almost equally exiled from those of the land." Count de Buffon (1812) Natural History. Volume 20. Translated by W Smellie, T Cadell, W Davies, London

Such was Buffon's summary of initial descriptions of penguins. Penguins are indeed anomalous birds. Their divergence from "typical" avian patterns is due to extensive adaptation to the marine environment. This separation from flying birds probably occurred in the Cretaceous period, over 65 million years ago (Simpson 1976). Like most orders of birds, penguins were clearly differentiated by late Eocene times (45 million years ago) (Simpson 1946, 1976) in which sea temperatures ranged from sub-tropical to cool temperate environments (Stonehouse 1969).

There are about eighteen extant species of penguins comprising six genera within the Order Sphenisciformes (Appendix 1, Stonehouse 1975, Walters 1980). Most controversy concerns the degree of taxonomic rank of the various populations of Eudyptula minor in New Zealand (Kinsky and Falla 1976, Meredith 1980). Within the Spheniscidae, the little penguin Eudyptula minor is regarded as the most conservative of penguins in terms of behavioural characteristics (Jouventin 1982) or on the basis of chemical composition of uropygial gland secretions (Jacob and Hoerschelmann 1981). The ecology and life history of the little penguin is well documented by Kinsky (1960), O'Brien (1940), and Richdale (1940) in New Zealand; Reilly (1975) and Reilly and Cullen (1979, 1981, 1982, 1983) in Victoria; and Hodgson (1975) and Warham (1958) in Tasmania.

Penguins are found across a broad range of latitudes in the southern hemisphere from the Equator to the Antarctic although their distribution is closely associated with cold water currents and food availability (Stonehouse 1967). The broad geographical range encountered by different species of penguins means that, contrary to popular belief, penguins are not uniformly subjected to cold exposure on land. Cold stress, however, is encountered by all penguins upon immersion due to the vastly enhanced cooling capacity of water compared to air.

Aquatic adaptation in penguins is clearly reflected in their external morphology. The stout fusiform or cigar-shaped body is streamlined to provide a very low drag coefficient in water (Nachtigall and Bilo 1980). The penguin wing is relatively narrow, short, and flat with little or no flexion at the elbow for propulsion through the dense medium of water (Clark and Bemis 1979). The short legs and feet, used as rudders in water, extend from the rear of the body and give the penguin its characteristic upright stance on land. This posture also confers an ambulatory or waddling gait on land which limits the penguin to low walking speeds with relatively high energy costs associated with large lateral displacements of the body in each stride (Pinshow et al. 1977).

Despite such morphological adaptations it is ironic that we know relatively little of the penguin's marine life style. Penguins may spend considerable time at sea, although they are constrained by their avian lineage to come ashore annually for the purposes of breeding and moult. During these periods penguins are separated from their food source and may undergo extensive fasts.

The distinctive morphological and ecological characteristics of penguins have long been recognized. Knowledge of the physiological characteristics associated with the penguin's aquatic lifestyle, however, are less clear. The little penguin is the smallest penguin species and hence the smallest flightless marine homeotherm. The relative ease of obtaining and maintaining these birds in captivity makes possible studies which could only be conducted with considerable difficulty and expense on Antarctic and sub-antarctic species. This study concentrates on the energetic relationships

between the little penguin and its environment in terms of thermoregulation and ventilation in air and water; the metabolic and insulative adjustments in response to wind; and the metabolic consequences and possible energetic savings due to sleep.

CHAPTER 1.

THE ENERGETIC PARAMETERS

Avian thermal biology is well served by a number of extensive reviews (Calder and King 1974, Dawson and Hudson 1970, King and Farner 1961) which detail patterns of heat production and heat loss by which birds maintain homeothermy. Within this framework the primary variables of animal energetics are metabolic heat production and body temperature. When combined they give an approximate rate of heat transfer (usually referred to as conductance) between an animal and its environment. Although extensively measured and compared among avian species, there remain a number of problems with the comparison and interpretation of these variables. This chapter serves as a review of these problems and a preview to the metabolic and thermoregulatory patterns in the little penguin presented in the following chapters.

1.1 Metabolic heat production

The literature on metabolism is voluminous. This area is well covered in reviews by Bartholomew (1977), Calder and King (1974), Kleiber (1961) and Schmidt-Nielsen (1970), amongst others. The preferred measure for comparison is standard metabolic rate, defined as metabolism per unit time, expressed in Watts. It is obtained from a resting, fasting, awake animal at thermoneutrality (Bligh and Johnson 1973) in the active or resting phase of its daily cycle.

Metabolic rate is positively correlated with body size. Metabolic rate (H) and body mass (M) follow the allometric scaling relationship:

$$H = aM^b \quad (1.1)$$

where b is the slope or mass exponent of the resulting linear regression and a is a constant which varies with the phylogenetic

lineage of different groups. It is generally accepted that the slope of scaling relationships between energy metabolism and body weight in diverse animal forms is close to 0.75 (Hemmingsen 1960, Kleiber 1961). This exponent, however, causes a good deal of distress amongst comparative physiologists due to doubts about its validity and meaning. Unfortunately, these problems do not appear to have any clear or immediate answer.

Although the ubiquity of the 0.75 mass exponent suggests some general underlying principle(s), explanation has eluded biologists. Most authors have approached the problem in terms of dimensional analysis (Stahl 1962) whereby changes in mass, length, and time are related to size. It has been long recognized that heat loss from an animal is proportional to its surface area (which scales as $M^{0.67}$) but energy produced is proportional to volume (ie. $M^{1.0}$) (Thompson 1942). The 0.75 mass exponent may be then considered a compromise between the two scaling relationships (Calder 1974). The choice of heat loss as the effective determinant, however, is unfortunate. As Schmidt-Nielsen (1975) points out, temperature regulation is not a problem for non-homeotherms, but many other physiological processes, such as oxygen uptake, depend upon surface area.

Since the exponent in the allometric equation is empirically derived, it is open to various methods of statistical interpretation. A recent analysis by Heusner (1982a) questions the validity of lumping data from different species into a common equation. Heusner suggests that within each (mammalian) species considered, the intraspecific mass exponent is 0.67 and argues that interspecific comparison lacks a uniform causal relationship due to differences between metabolically active tissues and structural components. However, if scaling of supporting tissues in animals of different sizes is considered a component of metabolic rate, then the 0.75 mass exponent should still retain significance. Feldman and McMahon (1983) argue that the 0.75 mass exponent emerges as a mean of both intra- and interspecific scaling factors.

A number of ingenious suggestions relate various physical principles to the empirically observed exponent such as resistance to elastic failure with increasing weight (McMahon 1973), gravitational

TABLE 1.1
ALLOMETRIC EQUATIONS FOR STANDARD METABOLIC RATE IN BIRDS.
METABOLIC RATE IN WATTS, BODY MASS IN KILOGRAMS

Sample	N	Wt. range (kg)	Equation	Reference
Passerines	48	0.003-1.0	$6.26M^{0.72}$	Lasiewki and Dawson (1967)
Nonpasserines	72	0.003-100	$3.80M^{0.72}$	idem
Passerines				
active	14	0.01-2.5	$6.83M^{0.70}$	Aschoff and Pohl (1970a)
rest	14	0.01-2.5	$5.57M^{0.73}$	ibid
Nonpasserines				
active	17	0.015-10	$4.41M^{0.73}$	ibid
rest	17	0.15-10	$3.56M^{0.73}$	ibid
Nonpasserines				
rest	24	0.027-1.2	$5.40M^{0.72}$	Prinzinger and Hanssler (1980)
Passerines				
summer, rest	41	0.009-1.2	$4.96M^{0.69}$	Kendeigh et al., (1977)
winter, rest	35	0.009-1.2	$4.94M^{0.65}$	ibid
Nonpasserines				
summer, rest	27	0.025-3.9	$4.21M^{0.73}$	ibid
winter, rest	14	0.117-4.0	$3.93M^{0.69}$	ibid
Ratites				
a	0.67-100		$2.83M^{0.73}$	Calder and Dawson (1978)

a Assuming a similar mass exponent to other birds.

tolerance (Economos 1979), or an operational time correction factor (Gunther 1975). By contrast to examination of mass and length changes with weight, Lindstedt and Calder (1981) suggested that since metabolic rate is expressed as volume per time, physiological time scales (in proportion to $W^{-0.25}$) may drive scaling since volumes and organs of capacity are constrained to scale as approximately $W^{1.0}$. Unfortunately there is little consensus amongst these hypotheses. Heusner (1982b) argues that different sized animals are not similar (hence they may not be compared by dimensional analysis), and that even in relationships due to similarity, it is not possible to determine a single causal factor since variables change together.

In summary, it appears that species may scale in a different manner to groups of species, and the choice of a single determinant scaling factor is simplistic. Since basal metabolism is an integral measure of physiology, there may well be a composite family of variables, each with its own power function, that combine to produce the enigmatic 0.75 mass exponent. In pragmatic terms, this empirical exponent can be accepted for predictive purposes.

1.1.1 Standard metabolic rate in birds

Despite a proliferation of allometric analyses of avian standard metabolic rates, the value of the constant a for birds in equation 1.1 is not uniform. As shown in Table 1.1 there is a wide variety of predictive equations available for comparison, unfortunately with no statistical comparison between equations.

Much of the variability between these allometric equations is due to greater metabolic intensity in birds of the Order Passeriformes when compared to other orders, loosely grouped as non-passerines (Lasiewski and Dawson 1967). This partition has recently been critized by Prinzinger and Hanssler (1980) who reported an elevated level of metabolism in relatively small non-passerines. However, since Prinzinger and Hanssler collected data at ambient temperatures of 20-25°C, it is not clear that small birds in their study were at thermoneutrality and hence experiencing basal

conditions.

The other major division accepted within avian metabolism is due to influence of the circadian rhythm. Aschoff and Pohl (1970a) demonstrated that metabolic rate varies with the activity phase of a bird's diurnal cycle. When combined with equations for passerine and non-passerine birds the equations of Aschoff and Pohl for activity/rest phase are usually taken as the standard for comparison. Division of Lasiewski and Dawson's equations into diurnal components provides essentially similar results.

Climate is also suggested to influence standard metabolic rate in birds (Dawson and Bennett 1973, Weathers 1979). Kendeigh, Dol'nik and Gavrilov (1977) recommended that avian metabolism be further subdivided into summer and winter components. Surprisingly, when I reanalyzed their data on a kilogram weight scale for comparison with other allometric equations in Table 1.1, no difference with season was observed. This disparity is a scaling effect. The difference in mass exponents between summer and winter indicate that small birds from the data of Kendeigh et al. increase their standard metabolic rates proportionally more than large birds during winter. Hence allometric equations based on gram body weight (where the constant predicts metabolic rate for a hypothetical one gram bird) show a substantial difference in metabolism between summer and winter. When scaled upon a kilogram body weight basis this difference disappears. Weathers and Caccamise (1977) also note that seasonal changes in metabolism appear to be minimal for large birds. Although the data of Kendeigh et al. show changes in metabolic intensity for the same species measured in summer and winter, changes in metabolic rate with season are not always apparent from other studies (Aschoff and Pohl 1970b, Chaffee and Roberts 1971, Saarela, Rintamaki, and Saarela 1984).

The mass exponent in the equation of Kendeigh et al. (1977) for passerines in winter reflects a surface scaling relationship (ie. $M^{0.66}$ instead of $M^{0.75}$). On this basis passerines may be more homogeneous in dimensions and follow a different set of scaling factors to the diverse range of shapes in non-passerines (after Heusner 1982). If valid, however, this result should extend to summer

acclimatized passerines and other passerine data sets in Table 1.1, a corollary that is not immediately apparent. As discussed above, increased metabolism in small passerines in winter appears responsible for this change in slope. Prinzinger et al. (1981) cite increased motor activity in small hummingbirds as a reason for lower mass exponents during the day in Apodiformes. A similar artifact for small passerines in winter in the analysis of Kendeigh et al. may result in the anomolous mass exponent.

Grouping non-passerines into a single assembly may, a priori, mask possible metabolic differences. A number of authors (eg. Calder and Dawson 1978, Wijnandts 1984, Zar 1969) have proposed further sub-division of the non-passerines into separate metabolic relationships for various taxonomic groups. Such fragmentation should be regarded with caution. The strength of allometric analysis relies on the quality of data and on the range of body weight employed (Lasiewski and Calder 1971). Many of the equations for single non-passerine orders are based on data with a weight range much less than the six orders of magnitude used for all non-passerines (Lasiewski and Dawson 1967).

The equation for ratites presented by Calder and Dawson (1978) is associated with special problems. These authors suggested that the lower level of metabolism in ratites and kiwis reflected a reduction in peak energy demands associated with the loss of flight. However, due to aerodynamic constraints very large birds are flightless and those at the upper end of the weight range for flight employ gliding rather than powered flight. If regarded as birds which per se reflect natural variation in form with increasing size, then ratites may be considered in general scaling analysis. However, if the argument for loss of flight is considered strong enough to segregate ratites from carinate flying birds in metabolic analysis, then there must be doubt about inclusion of other ratite variables (respiration, feather weight etc) in general avian allometric analysis.

Methodological variability is also inherent in any collection of data from different sources. Even within a generally accepted and standard equation for avian metabolism, there is considerable margin for error. Despite a correlation coefficient of 0.968, the equation

of Aschoff and Pohl (1970a) for non-passerines (active phase) contains a mean absolute prediction error of 14.8% (after Smith 1980). This uncertainty in individual data points, while not compromising the general relationship, makes it difficult to recognize potential differences in metabolism. The family of composite lines for each group of non-passerines probably encompasses the range of variability found in the equation for all non-passerines. However, it is rash to claim that only the well-recognized divisions in avian metabolism are valid. It is ironic that the search for more comparative data with its attendant scatter may mask variations in metabolic intensity with ecological or taxonomic variables.

1.2 Body temperature

Birds, as homeotherms, regulate their body temperature within relatively narrow limits despite variations in heat production and heat flux between the bird and its environment. However, no single measurement reflects the true whole body temperature (T_b) since the body consists of a series of thermal gradients ranging from a relatively stable deep body temperature to more labile temperatures at the surface or extremities. This variation between the body core and surrounding shell(s) depends upon sites of heat production, degree of vascular resistance, and countercurrent heat flow arrangements.

Since deep body temperature maintains the most stable thermal level it is used as a standard for comparison between individuals and species. Variation is still found between temperatures within the body core. Cloacal temperature is the most often used measurement in avian studies although Misson (1978) reported that it was lower than simultaneous measurements of tissues overlying the spinal cord. Oesophageal temperature has been suggested to be a good value of mean core temperature since it provides an indirect measurement of arterial blood leaving the heart (Edholm and Weiner 1981). These differences, however, are usually slight particularly when compared to variations in T_b within and between species.

In order for valid comparison, standard measurements of deep body temperature are needed. Various factors such as activity, stress, diurnal phase, and site of measurement are well recognized to influence T_b (Calder and King 1974, Dawson and Hudson 1970, Southwick 1971, Wetmore 1921). It is not surprising that King and Farner's (1961) recommendations for a "standard" deep body temperature parallel those for resting metabolism and where possible, these variables should be taken together.

Body temperature in resting birds appears to be nearly independent of body size with a mean (and perhaps abstract) value of 40 ± 1.5°C (Calder and King 1974). However, a number of nonpasserine orders which are flightless (ratites), marine (eg. penguins, Procellariiformes) or have species which employ torpor (Caprimulgiformes) have slightly lower body temperatures (Dawson and Hudson 1970). The reasons for these variations are not immediately clear. Although the ratites have relatively low basal metabolic rates (Calder and Dawson 1978), there is by contrast no difference in T_b between passerines and non-passerines. The diversity of life styles associated with a lower body temperature suggest several different causal factors.

The above discussions of metabolism and body temperature have been based on minimal values. Energetics of resting birds have been used a a baseline for analysis of energy consumption in natural environments (eg King 1974). Although measurements under controlled conditions are necessary for standard comparisons, it is also apparent that these data may be ill-defined in relation to the natural environment. Walsberg (1983) in an excellent review on avian ecological energetics notes that the allometric equation for daily energy expenditure in free-living birds scales in a different manner to basal metabolism. Small birds appear to operate at relatively higher levels of energy turnover than large birds in the wild partly due to increased activity, so that daily energy expenditure is not a constant multiple of basal metabolism. However, it is pertinent to note that the data for the largest bird in Walsberg's analysis, the emperor penguin, refers to fasting, breeding birds (Le Maho et al. 1976). More recent analyses of metabolism in free-living penguins

indicate that energy is used at approximately 2.5-3.0 times basal levels (Davis et al. 1983, Kooyman et al. 1982) although insufficient data are available to indicate whether this is a consequence of size or environment.

1.3 Conductance

Thermal conductance describes the ease of heat transfer between an animal and its environment. It is conventionally described in simplified terms as a linear proportion of the thermal gradient between body temperature (T_b) and environmental temperature (T_a) (vide Burton 1939). Hence:

$$\dot{H} = \dot{Q} = C(T_b - T_a) \quad (1.2)$$

where the rate of metabolic heat production ($\dot{H}$, Watts) is assumed to equal the rate of heat loss ($\dot{Q}$, Watts) during steady-state conditions. The variable C (W/°C) in equation (1.2) is a proportionality coefficient which represents total thermal conductance (Schmidt-Nielsen 1975). Conduction strictly describes heat transfer between solid surfaces in contact with each other so that C is more properly defined as a heat transfer coefficient (Calder and King 1974). Insulation (I) is the reciprocal of conductance and expresses the resistance to heat transfer.

The relationship given above is sometimes considered to represent Newton's Law of Cooling, which is unfortunate since equilibrium conditions are defined. Fourier's Law of Heat Loss which describes the rate of sensible heat exchange is often considered more appropriate (Kleiber 1961, Mount 1979) although Cena and Clark (1979) note that within the zone of thermoneutrality this is inapplicable since a bird changes its body conductance rather than heat production. It is apparent, however, that both theoretical frameworks describe heat loss as the product of a coefficient (conductance) and a temperature gradient.

The minimal level of heat transfer is a useful expression of

thermal adaptation to cold environments. Total conductance is often estimated as the slope of the regression between specific metabolic rate and ambient temperature below the thermoneutral zone (Bradley and Deavers 1980, Lasiewski et al. 1967, McNab 1980). This approach assumes that conductance is constant and minimal at low temperatures and that the metabolic line extrapolates to $T_a = T_b$ when $\dot{H} = 0$. Although many mammals fit this scheme fairly well (Scholander et al. 1950a,b) many birds have metabolic curves which extrapolate to temperatures above T_b (Calder and King 1974). This implies that conductance in birds may be further reduced below the thermoneutral zone. It is also apparent that conductance values obtained below the thermoneutral zone have no direct relevance to standard metabolism. Allometric equations for avian metabolism at 0°C follow different scaling factors to standard metabolism (Kendeigh 1970).

Conductance may also be derived by re-arranging equation (1.2) to:

$$C = \dot{H}/(T_b - T_a) \quad (1.3)$$

and calculating a mean value of minimal heat transfer from concurrent measurements of H, T_b, and T_a below the thermoneutral zone. This equation's accuracy is improved by subtracting the energetic equivalent of evaporative water loss ($\dot{E}$) from heat production to give dry heat transfer. Equation (1.3) then becomes:

$$C_d = (\dot{H} - \dot{E})/(T_b - T_a) \quad (1.4)$$

where C_d equals "dry" conductance or the sensible heat transfer coefficient. Heat loss, however, occurs across the surface of an animal. To represent conductance in physically correct terms as heat flux density ($W/(m^2.°C)$) equation (1.4) should be divided by the surface area (SA) of the animal to give:

$$C_d = (\dot{H} - \dot{E})/(T_b - T_a)SA \quad (1.5)$$

The surface area of animals is generally assumed to follow the scaling relationship:

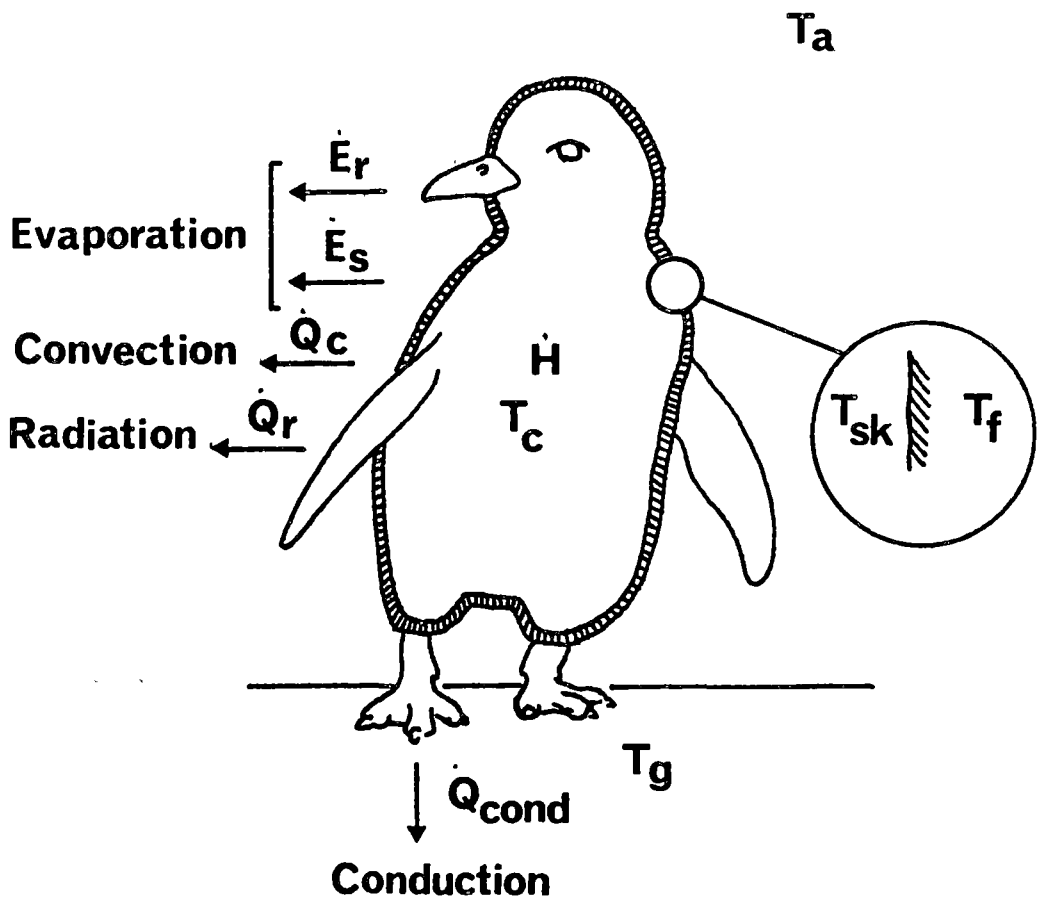

Figure 1.1 Pathways of heat loss from a bird to its environment. Metabolic heat production ($\dot{H}$) passes through the internal insulation between T_c (core temperature) and T_{sk} (skin temperature) and external insulation between T_f (outer coat temperature) and T_a(environmental temperature).

Non-evaporative heat transfer consists of convection ($\dot{Q}_c$) and radiation ($\dot{Q}_r$) from the birds surface, and by conduction ($\dot{Q}_{cond}$) to the ground at temperature (T_g). Evaporative heat loss consists of respiratory evaporative heat loss ($\dot{E}_r$) and cutaneous evaporative heat loss ($\dot{E}_s$). Evaporation depends primarily upon vapour pressure differences rather than temperature. Note that the environmental temperature for radiative exchange may differ from T_a. (From Mount 1979).

$$A_b = k.m^{0.667} \quad (1.6)$$

where k is known as the Meeh value. Walsberg and King (1978a) calculated surface areas in twelve species of birds over five orders of magnitude to obtain Meeh values of 10 for the skin surface area and 8.1 for the surface area of the feathers. The latter coefficient excludes the beak and non-feathered portions of the hind limbs. Although these areas are relatively insignificant in heat transfer at low temperatures due to peripheral vasoconstriction and heat exchange mechanisms, they increase in importance with increasing temperature (Hagan and Heath 1980, King and Farner 1961). Surface area may also change considerably with postural and behavioural adjustments such as feather erection (Hill et al. 1980).

The total heat transfer coefficient, as may be expected, is not a unitary value. As a measure of total heat flux it includes heat transfer coefficients for radiation, convection, conduction, and evaporation (Figure 1.1). Moreover, some modes of heat loss are not linear. Forced convective heat transfer varies with the square root of windspeed and radiative heat exchange depends upon the fourth power of the surface temperatures of the animal and its surroundings, the latter of which may differ considerably from air temperature. Evaporation is not driven directly by temperature but rather by differences in water vapour pressure between exhaled and inhaled air. Detailed analyses of heat transfer in animals may be found in Bakken (1976) and Gates (1980).

The simplified analysis of conductance (equation 1.5) also considers only the total thermal gradient to be maintained for homeothermy. When heat transfer is analysed in terms of a series of internal and external heat transfer coefficients, the external coefficient is found to be strongly influenced by environmental conditions (Tracy 1972). This implies that conductance is not an exclusive property of the animal but is partly determined by its environment (Bakken and Gates 1975). However, surface temperature measurements for calculation of external heat transfer may vary over the animal's surface and are difficult to achieve in conjuction with metabolism. Gates (1980) notes that in a metabolic chamber the environment is usually uniform giving a relatively constant surface

temperature.

In summary, while the conventional index of thermal conductance does not accurately describe the complexities of heat transfer, the alternative approach of quantifying each avenue of heat loss is impractical for general purposes. In pragmatic terms, the conventional approach is likely to continue being used (or misused) as a basis for analysis. Analysis of energy exchanges in the natural environment, however, requires that each mode of heat transfer be rigorously examined (Walsberg and King 1978b, Webb and King 1983)

1.3.1 Conductance in birds

Minimal conductance is most often compared between birds as a measure of cold resistance. Heat transfer coefficients in heat-stressed birds, however, follow a different pattern and rely less on sensible heat transfer as evaporation and ventilatory adjustments are important in thermoregulation at high ambient temperatures (Dawson 1982, Weathers 1981).

There are a number of predictive equations relating minimal thermal conductance to body weight in birds (Table 1.2). Calder and King (1974) and Calder (1974) combined two commonly used relationships (Herreid and Kessel 1967, Lasiewski, Weathers, and Bernstein 1967) to provide equations for passerines and nonpasserines. If each set of relationships in Table 1.2 is taken as valid then the level of minimal heat transfer in birds varies with taxa, season, and circadian influence, thereby paralleling these differences in standard metabolic rate. Although the mass exponents of these equations cluster around 0.50, there is considerable diversity in their constants.

Increased data might be assumed to confer more precise estimates of the variable in question. But as shown in Table 1.2, the diversity of equations for conductance in birds appears to have led to the situation where comparison of empirical data with predicted relationships becomes specious. Drent and Stonehouse (1971) produced an extensive tabulation of minimal conductance in birds but did not

TABLE 1.2 ALLOMETRIC EQUATIONS FOR MINIMAL HEAT TRANSFER COEFFICIENTS IN BIRDS

(C in mW. $°C^{-1}$, Body mass in grams)

Sample	N	Wt. range (grams)	Equation	Reference
Passerines	-	-	$5.29m^{0.46}$	Calder (1974)
Nonpasserines	-	-	$4.72m^{0.46}$	ibid
Passerines				
summer, night	41	8.9-1,203	$4.10m^{0.53}$	Kendeigh et al., (1977)
winter, night	35	8.8-1,208	$3.53m^{0.54}$	ibid
Nonpasserines				
summer, night	30	25.2-3,900	$3.13m^{0.57}$	ibid
winter, night	12	117-4,010	$2.22m^{0.59}$	ibid
Passerines[a]				
active	28	6.0-1,130	$4.78m^{0.54}$	Aschoff (1981)
rest	26	10.3-360	$3.22m^{0.54}$	ibid
Nonpasserines[a]				
active	39	2.7-2,430	$5.28m^{0.52}$	ibid
rest	11	40.0-2,020	$5.29m^{0.42}$	ibid

a Assuming 1 ml $O_2 g^{-1} h^{-1}$ = 20.1 joules

construct a predictive relationship since they found considerable scatter in the original data and regarded this as reflecting the plasticity of heat transfer coefficients in metabolic adaptation (Scholander et al. 1950a). Although conductance may be non-uniform, it is perhaps not unmanageable. A useful step would be for authors constructing such equations to statistically compare their contructs with those already existing.

In addition to adaptive differences in conductance, scatter may be derived from conditions of measurement and methods of analysis. Much of the data in the above equations (Kendeigh et al. 1977, Lasiewski et al. 1967) is derived from the slope of the regression between metabolic rate and ambient temperature below the thermoneutral zone. Kendeigh et al. (1977, their Appendix 5.1) note that the adjustment of regression lines was commonly made to force the regression through H=0 at body temperature. As noted previously, this approach is inappropriate and it appears to have resulted in very low estimates of heat transfer. The data of Herreid and Kessel included in Calder and King's analysis is partly derived from cooling curves of dead birds and thereby does not account for physiological components of heat transfer.

Calder and King (1974) analyzed conductance data from the compilation of Drent and Stonehouse (1971) which accounted for evaporative heat loss to give the sensible heat transfer coefficient. When expressed in terms of surface area from the equation of Walsberg and King (1978a) sensible heat transfer coefficient in birds is predicted as:

$$C_d = 0.46\ w^{-0.15} \quad (1.7)$$

where C_d is $mW/(cm^2.°C)$ and w is body weight (g). This equation contains a combination of derived variables (evaporative heat transfer, surface area) and thereby is as least as enigmatic as those given in Table 1.2.

There have been a number of attempts to explain the scaling of minimal conductance to the 0.5 power of bodyweight. Conductance, in the strict sense, may be expressed (after Kleiber 1972) as:

$$C = kA/L \quad (1.8)$$

where k is conductivity (W/(m.°C)), A is surface area (m^2), and L is the thickness of the insulating cover (m). Kleiber assumed that in mammals L is proportional to $m^{0.2}$ (based on measurements of skin thickness) and that conductivity of the pelt was nearly constant. Hence conductance (as W/°C) equals $m^{0.67}/m^{0.20} = m^{0.47}$.

Kendeigh et al. (1977) argued that plumage thickness would be proportional to the ratio of plumage weight and surface area, as $m^{1.0}/m^{0.67} = m^{0.33}$. The number of feathers varies as $m^{0.18}$ so air trapped within the feathers (in proportion to thermal conductivity of the plumage) would change with body mass as $m^{0.33}/m^{0.18} = m^{0.15}$. Combining these exponents in the form of equation (1.8) then gives conductance as proportional to $m^{0.48}$. This analysis, however, is dimensionally doubtful. The ratio of plumage weight (g) to surface area (m^2) respectively gives thickness and thermal conductivity in terms of g/m^2 rather than a measure of length (m) or heat flux per unit length per degree temperature (W/(m.°C)). Inserting the dimensions from the analysis of Kendeigh et al. into equation (1.8) expresses heat transfer in the improbable units of m^{-2}.

Both the analyses of Kleiber and Kendeigh et al. are based on heat flux through the plumage. This approach is valid only if the plumage insulation is much greater than body and environmental insulation (cf section 4.4.2). Cena and Clark (1979) note that conduction through animal coats (equation 1.8) is not the sole means of heat transfer since thermal conductivities of animal coats are greater than still air; and radiation and convection substantially contribute to heat loss.

1.4 Resume and organization of the thesis

Metabolic rate and minimal conductance in birds vary systematically with body weight and are correlated with a number of taxonomic and ecological variables. Body temperature in birds remains relatively constant although penguins are noted to have a lower body temperature in comparison to most birds. Although this framework provides a useful basis for avian thermoregulation it is often

difficult to show distinctive physiological adaptations of a group of birds to their environment. For example, there seems to be no major physiological differences between desert as contrasted to non-desert birds (Crawford and Schmidt-Nielsen 1967). Due to their extensive adaptation to an aquatic environment, however, the pattern of energetic parameters in penguins are of considerable interest and may be expected to diverge considerably from other birds.

The aquatic lifestyle of penguins imposes several immediate environmental challenges. Due to the vastly different thermal capacities of air and water detailed patterns of heat loss and heat production in the little penguin in both environments are presented in Chapter 2. Penguins are diving birds with a respiratory system that is simpler in structure than in birds capable of flight. Chapter 3 examines the pattern of ventilation at different air and water temperatures and investigates its efficiency in relation to metabolic and thermoregulatory demands.

Temperature is the most widely used variable when examining thermoregulatory capacity. Other internal and external factors, however, are also important in thermal exchange. Wind is an integral part of the external environment and its effect upon metabolic rate and partitional insulation is discussed in Chapter 4. Although the effect of circadian phase upon metabolic rate in birds is well-known the potential effect of sleep upon this cycle and temperature regulation is not clearly defined. The biology and physiology of sleep is introduced in Chapter 5 and the influence of sleep upon metabolic rate and temperature regulation in the little penguin is examined in Chapter 6.

CHAPTER 2.

TEMPERATURE REGULATION IN AIR AND WATER

2.1 INTRODUCTION

Penguins as the most aquatic representative of birds are distinguished by distinctive morphological adaptations to their aquatic environment such as a dense coat of water-proof feathers and short wings modified as paddles (Stonehouse 1967, 1970). Despite such modification there has been comparatively little work on the thermoregulation of penguins compared with other birds and that mostly on large antarctic species (Le Maho et al. 1976, Pinshow et al. 1976).

Water represents an extreme thermal environment for a homeotherm. The reasons most often given are that water has a specific heat 1,000 times that of air and thermal conductivity 25 times that of air (Bullard and Rapp 1970). Moreover, the high viscosity and density of water gives a greatly reduced thermal boundary layer (Erskine and Spotila 1977). Although most penguins spend at least half their lives at sea the few studies which have investigated the thermal demands in water indicate that their aquatic lifestyle is metabolically expensive (Barre 1981, Kooyman et al. 1976).

The little or fairy penguin Eudyptula minor is the smallest penguin species and hence can be regarded as the smallest flightless marine homeotherm. Because of the distribution of the little penguin in temperate areas and its relatively small size it is an interesting species to compare with the larger antarctic and sub-antarctic penguins which are presumably more cold-adapted. Furthermore, the large surface area to volume ratio of the little penguin makes it of considerable interest to examine the metabolic and thermoregulatory consequences of immersion.

2.2 MATERIALS AND METHODS

2.2.1 Metabolic rate.

Metabolic rates in air and water were measured with a positive pressure open-circuit system (after Nicol 1976, Nicol and Maskrey 1980). The metabolic chamber consisted of an insulated 25l double-walled fibreglass container in which temperature was controlled by circulating brine through the outer annulus and a heater/cooler unit. Air flow rates through the chamber (2.9-4.4 l/min STP in air, and 3.8-8.9 l/min STP in water) were measured with a Gilmont flowmeter calibrated against a Tissot spirometer. Air space above the water in water experiments was 9.6 litres.

A variable speed blower passed chamber air through tubes of silica gel and soda lime to remove water vapour and CO_2. Air pressure in the chamber was shown by a manometer and normally maintained at 10-12 cm water to avoid dilution of the system from atmospheric air.

Outlet air was dried and passed to the sample channel of a Taylor Servomex OA 184 oxygen analyzer. Atmospheric air simultaneously passed through a flow meter and silica gel to the reference channel of the analyzer. Outputs from the sample and reference channels were compared by a Servomex RB-228 ratio box and recorded on a Rikadenki recorder with full scale deflection of 20 to 21% oxygen. Oxygen consumption was calculated after Hill (1972). In some experiments the soda lime absorbent was removed from the system allowing CO_2 production to be measured with a Morgan Infra-red CO_2 analyzer or a Beckman LB-2 Medical Gas Analyzer. Gas analyzers were calibrated with high purity gas mixtures (Commonwealth Industrial Gases Ltd) and ambient air.

Mean respiratory quotient (± standard deviation) in air was 0.73 ± 0.03 (n=13) and in water was 0.74 ± 0.07 (n=67). Assuming an energetic equivalent of 19.7 kJ per l O_2, then 1 ml O_2/(g.h) is equivalent to 5.48 W/kg.

2.2.2 Body temperatures

Body temperature was continuously recorded by ingested radiotransmitters (Minimitter) or by an ensheathed 36 SWG thermocouple inserted 12-15 cm in the oesophagus of the penguin and taped to the lower mandible. In some experiments a discrete body temperature was taken at the end of an experiment by this method. Cloacal temperatures were recorded by 42 SWG thermocouples glued at specific lengths within a plastic sheath. At ambient temperatures above the upper critical temperature in air a thermocouple inserted 5-7 cm in the cloaca was used to avoid interference with respiratory patterns.

Feathered skin temperature was measured by a 42 SWG thermocouple glued to skin overlying the sternum. Foot temperature was measured with a thermocouple taped to the top of the middle toe and wing temperature was measured from a thermocouple taped to the inside of the leading edge of the wing at the distal end of the humerus.

Thermocouples and radiotransmitters were calibrated against a thermometer traceable to a National standard in a constant temperature bath. Thermocouple outputs were displayed on a Leeds and Northrup Speedomax 250 recorder. The signal from the radiotransmitters was measured from a stopwatch as time per 100 pulses.

2.2.3 Surface area

External surface area (excluding beak, legs, and feet) was measured on two little penguins (0.94 and 1.05 kg) by coating the frozen carcass with parafilm. This was then traced onto standard weight paper and weighed. Surface area thus determined was found to be 815 and 921 cm^2 which gave a mean Meeh value of 8.7.

2.2.4 Experimental procedure

Penguins were fed between 16:00 and 17:00 h in the afternoon before an experiment was commenced the following day. Details of penguin maintenance in captivity are given in Appendix 2.

Measurements during the day were taken between 10:00 and 18:00 h. Several experiments were also done at night within thermoneutrality in air for measurement of circadian effect upon standard metabolism . Determinations of oxygen consumption were made from the smallest decrement between inspired and expired chamber fractional oxygen content in chart records from unrestrained birds over periods of at least 15 min when the bird was resting quietly in the chamber in experiments in air or floating quietly in the chamber in water experiments. At least one hour was allowed for the penguin to equilibrate to the chamber temperature. Chamber temperature was not adjusted more than 10°C in each experiment. Measurements represent steady-state conditions, as indicated by a stable body temperature, except for very cold water temperatures and high air temperatures where the little penguins were unable to equilibrate.

Unless otherwise stated, mean body weight during experiments in air was 0.90 $\pm$ 0.09 kg (range 0.79 - 1.13 kg) and 1.0 $\pm$ 0.08 kg (range 0.91 - 1.24 kg) during experiments in water.

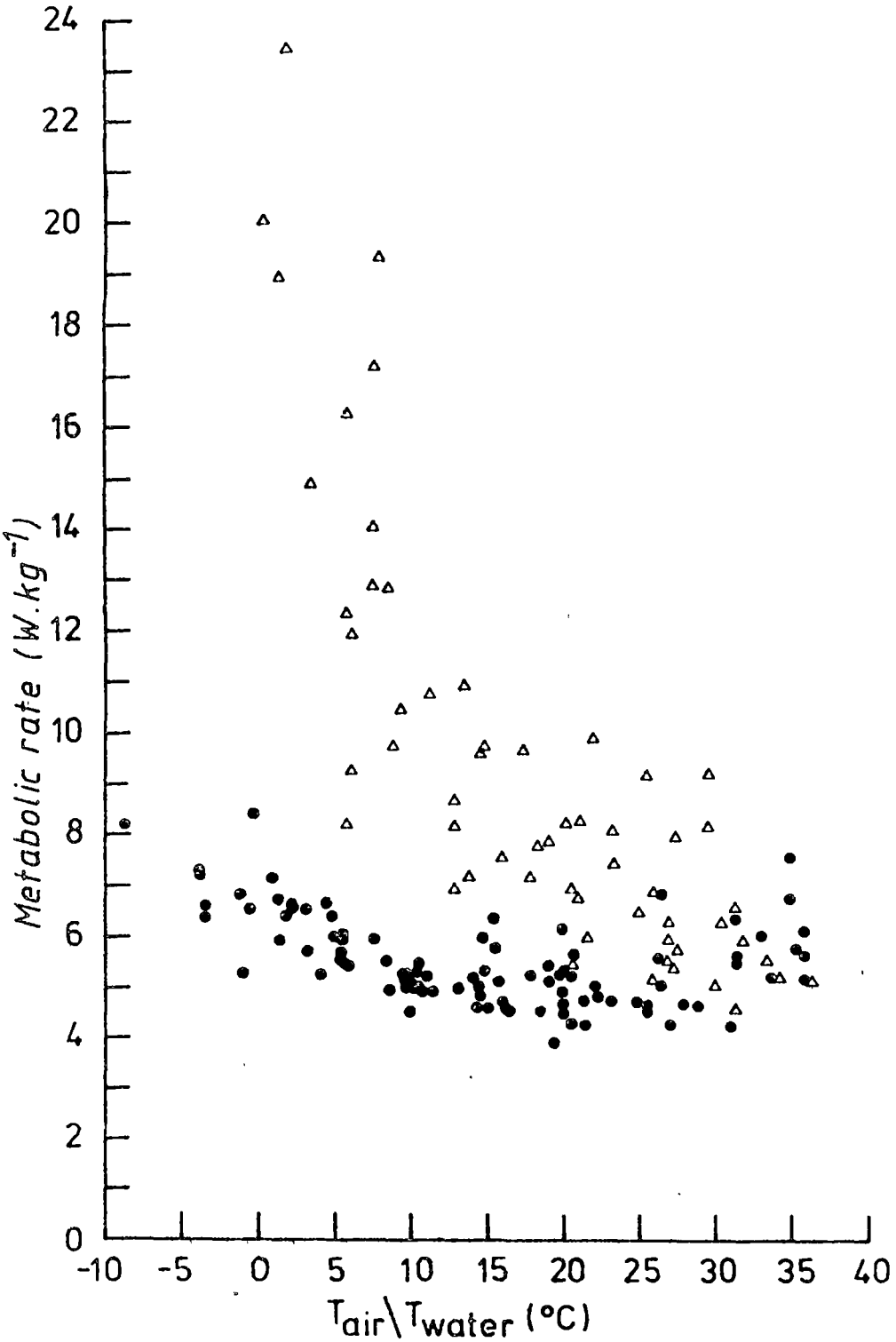

Figure 2.1. Metabolic heat production of resting little penguins at various air and water temperatures. Circles: air; triangles: water.

2.3 RESULTS

2.3.1 Metabolic heat production

Rates of heat production (H) of resting little penguins at air temperatures from -9 to 36°C and water temperatures from 0.3 to 36°C are shown in Figure 2.1.

In air the basal or standard metabolic rate at thermoneutrality (± SD) was 4.93 ± 0.39 W/kg during the day (n=41). At night standard metabolism was decreased to 4.64 ± 0.2 W/kg (n=10, mean body weight 0.77 kg) Minimal observed metabolic rates from each penguin were 3.96 ± 0.28 Watts during the day (n=6, 0.85 kg) and 3.51 ± 0.63 Watts during the night (n=4, 0.78 kg).

Metabolic heat production increased with cold exposure. Although the transition between minimum heat production at thermoneutrality and increasing metabolism in response to decreasing air temperatures is likely to be curvilinear rather than abrupt, an effective lower critical temperature (T_{lc}) was obtained by comparing pooled mear squares from a range of regression lines (Pinshow et al. 1976). From this method T_{lc} was estimated to be approximately 10°C. The relationship between heat production (H) and ambient temperatures below T_{lc} is given by the equation:

$$H\ (W/kg) = 6.71 - 0.17T_a \quad (2.1)$$

(n=35, r=-0.84, p . 0.001)

where T_a is ambient air temperature. Above air temperatures of approximately 30°C, however, metabolic rate increased sharply; and at 35°C the penguins appeared distressed and became hyperthermic.

Rates of heat production from penguins floating quietly in water show a different pattern to that seen in air. Heat production gradually increased with decreasing water temperature until a critical water temperature was reached whereupon the metabolic cost to maintain homeothermy became increasingly expensive. Comparisons of

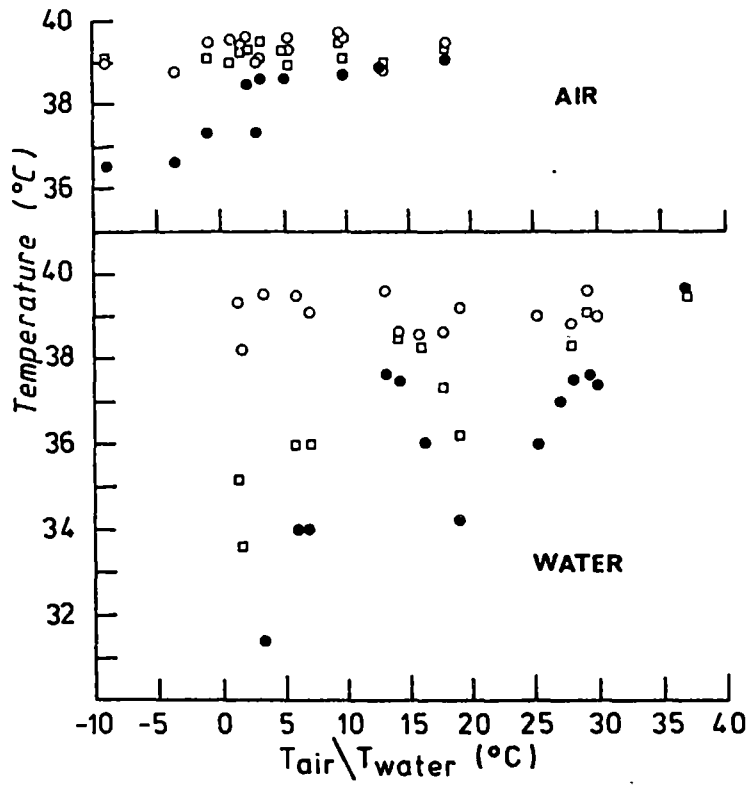

Figure 2.2. Cloacal and core temperatures in little penguins at various air and water temperatures. Results from 32 experiments on four birds. Open circles: core temperature; open squares: 5cm cloacal temperature; solid circles: 3cm cloacal temperature.

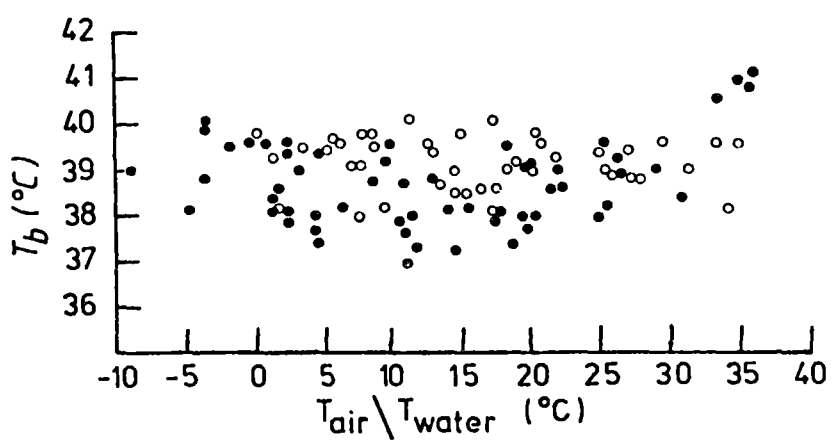

Figure 2.3. Core temperatures (represented by oesophageal or stomach temperatures) of little penguins at various air and water temperatures. Solid circles: air; open circles: water.

pooled mean squares from regression lines relating metabolism to water temperature indicate that this breakpoint lies at approximately 10°C. Above this water temperature the equation relating heat production to water temperature was:

$$H\ (W/kg) = 10.30 - 0.16T_w \quad (2.2)$$

$(n=34,\ r=-0.61,\ p < 0.001)$

where T_w is water temperature. Below 10°C the corresponding equation was:

$$H\ (W/kg) = 23.72 - 1.49T_w \quad (2.3)$$

$(n=17,\ r=-0.72,\ p<0.005)$

2.3.2 Body temperature

The relationship between cloacal and simultaneous measurements of core temperature (T_b, represented by oesophageal temperature or obtained by telemetry) in air and water is shown in Figure 2.2. In air, 5cm cloacal temperature remained relatively constant with decreasing air temperature and did not differ significantly from T_b ($t=0.49$, $n=26$, $p < 0.5$). Cloacal temperatures measured at a depth of 3cm, however, diverged markedly from T_b. This difference increased with decreasing air temperature so that at -10°C 3cm cloacal temperature was 2.5°C below T_b. In water, all cloacal temperatures diverged from T_b with decreasing water temperature. At a water temperature of 3°C, 3cm cloacal temperature was approximately 8°C below T_b. This difference may have been accentuated by water leaking into the cloaca beside the plastic sheath.

Core temperatures of little penguins at various air and water temperatures are shown in Figure 2.3. Mean T_b within the thermoneutral zone in air was 38.4 ± 0.8°C. At corresponding water temperatures, however, T_b was significantly higher at 39.2 ± 0.5°C ($t=4.41$, $n=50$, $p < 0.001$). In air below T_{lc} body temperature was elevated to 39.0 ± 0.8°C.

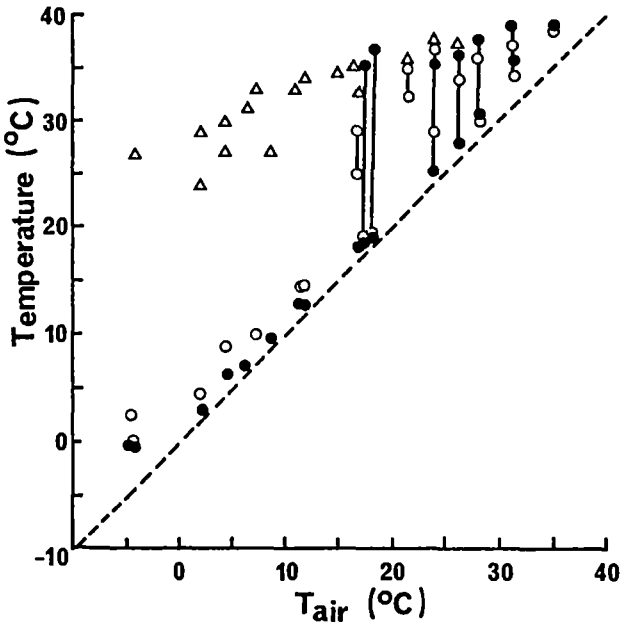

Figure 2.4. Skin temperatures of little penguins in air. Dashed line indicates isothermality. Results from eight experiments with four birds. At least two replicates for three birds and a single experiment for bird four as foot temperature at -4.1°C. Triangles: ventral feathered skin temperature; Solid circles: foot temperature; Open circles: wing temperature.

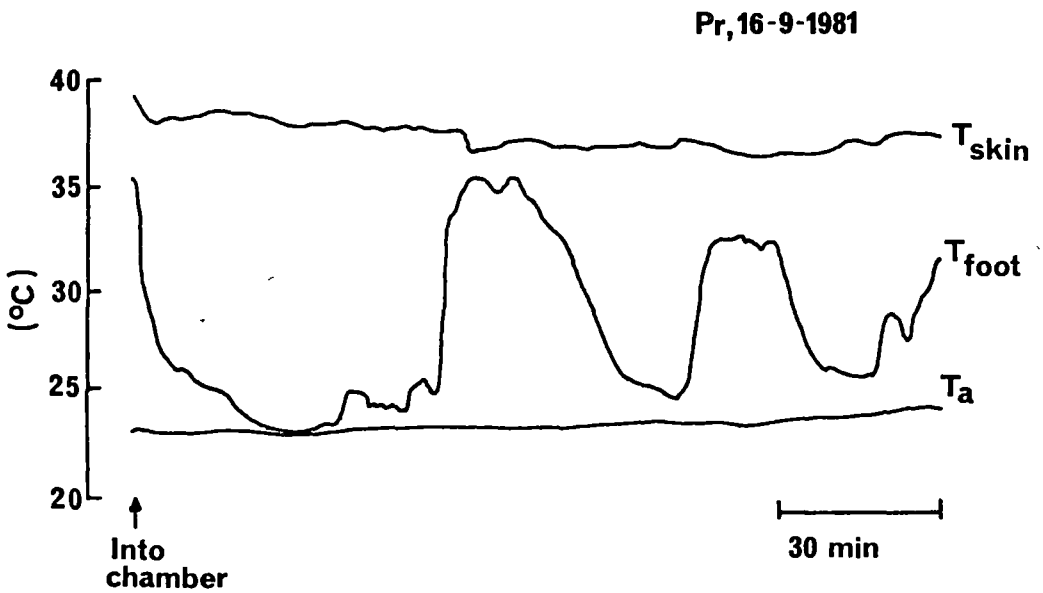

Figure 2.5. Typical record of feathered skin and foot temperatures of a little penguin at thermoneutrality. Feathered skin temperature remains stable whereas foot temperature reflects peripheral vasomotor shunts.

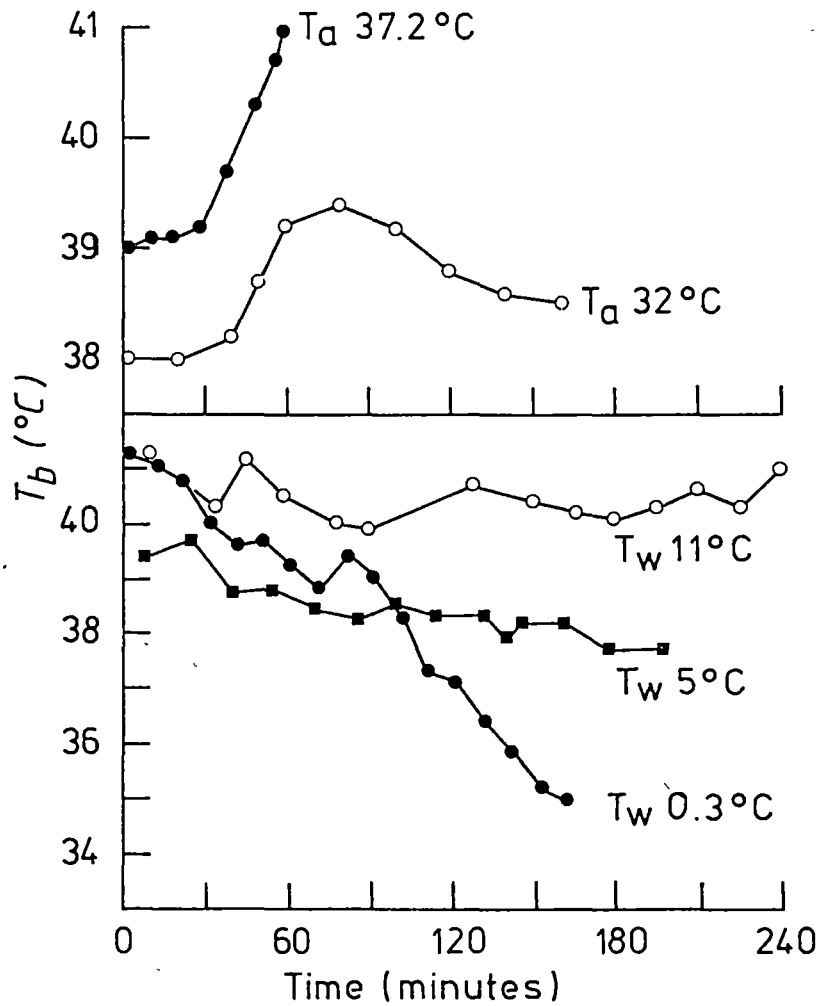

Figure 2.6. Changes in core temperature of little penguins with time at various air and water temperatures. Results from five experiments with two birds. T_a air temperature; T_w water temperature.

Skin temperatures of little penguins in air are shown in Figure 2.4. Feathered skin temperatures decreased slowly with air temperature. Temperature of the wings and feet remained very close to air temperatures up to approximately 15-20°C. Above this temperature there was a marked change in pattern as the peripheries alternated between vasoconstriction and vasodilatation (Figure 2.5). At increasing air temperatures above this breakpoint progressively more time was spent with the flippers and wing vasodilated. Skin and peripheral temperatures are not given for different water temperatures. Foot and wing temperatures were very close (0.1°C) to water temperature but it is difficult to get true surface temperature in water (Boutelier et al. 1977). Measurements of feathered skin temperature in water are likely to be underestimated due to water leaking into the plumage along the thermocouple.

Little penguins could not stand prolonged exposure to heat stress or very cold water. The results of five experiments showing changes in T_b at these thermal extremes are given in Figure 2.6.

2.4 DISCUSSION

2.4.1 Body Temperature

Deep body temperature of the little penguin at thermoneutrality (38.4°C) in this study lies within the range of body temperatures previously compiled for penguins (Dawson and Hudson 1970). This value is similar to that found for little penguins by Baudinette, Gill and Driscoll (unpubl. manuscript) and also to the mean cloacal temperature (38.6°C) reported for six little penguins by Morgan (1916). The latter agreement, however, is probably fortuitous, since in Morgan's words "...all the birds naturally struggled when captured but none appreciably more than another." Cloacal temperatures for two little penguins also obtained by Morgan (in White 1916; cited in Wetmore 1921, McNab 1966) were relatively high: 39.2°C and 42.7°C. These values are not comparable since the birds were moulting and their temperature was presumably taken in a similar manner to Morgan (1916).

Body temperatures in the little penguin are similar to those reported for the largest penguin species, the emperor penguin (Table 2.1) and as such, provide no support for the claims that body temperature in penguins is inversly related to body size (Bougaeff 1974, Mougin 1974).

As a group penguins have low core temperatures in comparison with other birds (Dawson and Hudson 1970, King and Farner 1961, McNab 1966). However, it has been suggested that a low T_b in penguins may be due to the site of measurement as stomach temperatures were found to be 0.6-5.0°C higher than simultaneous measurements of cloacal temperature in four species of penguins (Barre 1980, Calder and King 1974, Goldsmith and Sladen 1961, Mougin 1972, 1974).

A compilation of deep body and cloacal temperatures in penguins derived from the literature is presented in Table 2.1. Although the majority of the data represents Antarctic species (notably the emperor and Adelie penguins) values are presented for 14 of the extant 18 species of Sphenisciformes (Stonehouse 1975) which cover

TABLE 2.1 PENGUIN BODY TEMPERATURES

SPECIES	Wt (kg)	N	T_{cl} (°C)	T_b (°C)	REFERENCE
Aptenodytes forsteri	26	2	-	38.6	Boyd and Sladen (1971)a,c
A. forsteri	23.4		37.8	-	Pinshow et al. (1976)b
A. forsteri	25.1		-	38.2	Le Maho et al. (1976)a
A. forsteri	26.3	1	-	38.1	Jarman (1973)a
A. forsteri	-		-	38.5	Bougaeff (1974)a
A. forsteri	-		37.2	-	Mougin (1966)a
A. patagonica	-	28	37.7	-	King and Farner (1961)a
A. patagonica	14.6	11	38.6	39.2	Mougin (1974)a
A. patagonica	12.7	12	38.1	38.7	Barre (1980)a
A. patagonica	11.1	8	37.4	-	Gavrilov (1977)b
Pygoscelis adeliae	4.4	2	-	38.4	Boyd and Sladen (1971)a,c
P. adeliae	-	115	38.5	-	Prevost and Sapin-Jaloustre (1964)a
P. adeliae	4.0	11	-	38.9	Kooyman et al.(1976)b
P. adeliae	-	23	38.9	-	Eklund (1942)a,d
P. adeliae	3.3		-	38.8	Murrish (1973)b
P. adeliae	-		-	39.0	Goldsmith and Sladen (1961)b
P. adeliae	-		-	40.0	Bougaeff (1974)a
P. adeliae	3.5	22	38.5	-	Murrish (1982)b
P. papua	-	33	38.1	-	King and Farner (1961)a
P. papua	-		-	39.8	Mougin (1974)a
P. papua	4.9	11	38.3	-	Murrish (1982)a
P. papua	5.2	1	-	39.2	Stahel (unpub)a,c
P. antarctica	3.1	8	39.5	-	Murrish (1982)b
Megadyptes antipodes	3.7	13	37.8	-	Farner (1958)a
Eudyptes chrysolophus	-	1	-	40.0	Mougin (1972)a
E. chrysolophus	3.9	4	37.7	-	Gavrilov (1977)b
E. sclateri	3.6	9	38.6	-	Warham (1972)a
E. crestatus	2.3	2	37.9	-	Gavrilov (1977)b
E. crestatus	3.5	2	-	38.1	Stahel (unpub)a,c
E. pachyrhynchus	4.3	32	37.7	-	Warham (1974)a
Spheniscus mendiculus	2.2		39.7	-	Boersman (1975)a
S. humboldti	3.9		-	39.0	Drent and Stonehouse (1971)b
S. demersus	3.2		-	38.6	Frost et al.(1976)a,c
S. demersus	-		-	39.0	Erasmus and Smith (1974)a
Eudyptula minor	1.0		38.6	-	Morgan (1916)a
E. minor	1.1	6	-	38.4	This study b

T_{cl} is cloacal temperature; and T_b is core or deep body temperature

a Field; b. Lab; c Telemetry; d Mean of minimum and maximum values

N = number of species

the range of weight and geographical distribution within the group. It is difficult to provide some measure of comparison between these reported values. Body temperature is not a constant characteristic of an animal since it varies with time of day, season, and activity (Calder and King 1974, Dawson and Hudson 1970). In addition to possible differences between continuous measurement and the "grab and jab" technique, there is some evidence that the level of body temperature in penguins varies with the stage of the life cycle (Boyd and Sladen 1971, Prevost and Sapin-Jaloustre 1964). An increase in T_b during moult is well recognized (Groscolas 1978) and moulting values have not been included in this analysis. I have also excluded the cloacal measurements of Prevost and Sapin-Jaloustre (1964) for fasting emperor penguins since these are extremely low by comparison with other cloacal temperature data.

Despite such inherent scatter, there is a significant difference between mean cloacal (38.2 ± 0.7°C) and mean deep body temperatures (38.9 ± 0.6°C) in Table 2.1 ($F_{1,36}$ = 9.56, $p < 0.005$). Although there is a difference between cloacal and core temperatures, this analysis indicates that deep body temperature of penguins is indeed below that of most birds which have a body temperature of approximately 40°C (Dawson and Hudson 1970).

This study demonstrates that the discepancy between cloacal and deep body temperature is due to the cloaca comprising part of the peripheral shell which varies with ambient temperature and internal heat load. Hence many of the previous reports of cloacal temperatures in penguins are derived from probes not inserted deeply enough to penetrate the body core. Figure 2.2 shows that cloacal temperature 5 cm from the vent in the little penguin in air represents T_b whereas temperatures at 3 cm within the cloaca reflected changes in the temperature gradient between the probe and environment. Dissection of a little penguin revealed a well developed sphincter between the copradaeum and urodaeum/proctodaeum about 2.5 cm inside the vent. Difficulty in inserting a cloacal probe past this second sphincter could well result in many studies only reporting shallow cloacal temperatures which diverge from core temperature with cold stress. Differences between cloacal and core temperatures have also been reported for the white-crowned sparrow (Southwick 1973), chicken

(Misson 1978) and burrowing owl (Coulombe 1970).

The elevated core temperatures found in little penguins at low air temperatures and in water may be due to increased heat production and peripheral vasoconstriction as was suggested for the platypus by Grant and Dawson (1978). An increase in T_b with cold stress has also been reported for winter acclimatized mute swans and black grouse (Bech 1980, Rintamaki et al. 1983). However, T_b in water remained constant despite high levels of metabolism at low water temperatures and was unchanged at water temperatures above 30°C where heat production approached the basal levels found in air. This suggests that penguins in water may alter the set point for body temperature regulation. An elevated level of T_b in king penguins during immersion was reported by Barre (1981) whereas Kooyman et al. (1976) recorded a slight decrease in T_b in immersed Adelie penguins.

2.4.2 Metabolic Heat Production

The basal or standard metabolic rate of the little penguin can be compared with that predicted for other birds from the equation of Aschoff and Pohl (1970a). Their equation predicts a SMR of 4.08 W for a hypothetical 0.9 kg non-passerine bird in its active phase of the diel rhythm, a value that is 8.8% lower than this study (4.44 W) and 2.93 W for a 0.77 kg nonpasserine during its rest phase, 22% below values measured for the little penguin at night (3.57 W). Minimal observed values of standard metabolism were closer to predicted levels as these were 2% greater during the day and 18% greater at night. Considering the prediction errors inherent in allometric equations it appears that there is little difference between the standard metabolism of the little penguin and that expected for similar sized birds during the day.

Standard metabolism at night, however, diverged to a greater extent from prediction and may reflect the little penguin's polyphasic sleep patterns (cf Chapter 6). Although use of minimal observed values of standard metabolism gives slightly lower levels of energy expenditure, it also restricts number of data. Mean values from all experiments within thermoneutrality have been used in

comparing metabolism in the little penguin with other species.

There have been few reports of heat production from penguins in water. Unfortunately, both the studies by Barre (1981) on king penguins and Kooyman et al. (1976) on Adelie penguins used restrained birds that were fully immersed. As a result rates of heat production from these sub-antarctic and antarctic birds are high when compared to the little penguin. At a water temperature of 10°C the heat production of Adelie penguins (mean weight 4.0 kg) was 13.4 $W.kg^{-0.73}$ and approximately 15.2 $W.kg^{-0.73}$ for the king penguin (using a mean body weight for the species from Stonehouse (1975)). By comparison, heat production of little penguins in this study was 8.7 $W.kg^{-0.73}$ at the same water temperature. Baudinette and Gill (unpublished manuscript) give metabolic rate of little penguins resting in water of approximately 20°C as 6.40 $W.kg^{-1}$, slightly below that predicted for little penguins in this study at the same temperature (7.1 $W.kg^{-1}$) but within the scatter of data in Figure 2.1. Butler and Woakes (1984) reported that the metabolic rate of peruvian penguins (4.6 kg) resting in water at 16°C to be 6.41 $W.kg^{-0.73}$ which is similar to the level for the little penguin.

2.4.3 Metabolism in Sphenisciformes

The general level of metabolism in penguins has recently attracted interest on the basis of potential variation in avian metabolic rate with climate (Ricklefs and Matthew 1983, Weathers 1979) or as a reference for ecological energetics (Croxall 1982). Comparisons of metabolic intensity of penguins compared to other birds have given conflicting conclusions. Ricklefs and Matthew (1983) claim a relatively high level of standard metabolic rate in penguins, whereas Croxall (1982) and Brown (1984) concluded that penguins have similar relationships between metabolic rate and body size to that found in other birds.

Since penguins are widely distributed in the southern hemisphere, the concept that they may be uniformly subjected to considerable cold stress in terrestrial environments is somewhat misleading. Stonehouse (1967, 1970) provides a detailed account of the geographical distribution of penguins. However, penguins are

TABLE 2.2
COMPARISON OF OBSERVED AND PREDICTED RATES OF STANDARD METABOLISM IN PENGUINS

SPECIES	MASS (kg)	N		H_{sm} (Watts) Obs	$Pred_a$	$\%Pred_b$	REFERENCE
Aptenodytes forsteri	23.37	5	.	42.07	43.87	96	Pinshow et al.(1976)
A. patagonicus	11.08	4	-	21.9	-	-	Gavrilov (1977)
Pygoscelis papua	6.29	4	-	18.6	-	-	Adams and Brown, in Brown (1984)
P. adeliae	3.97	13	.	12.27	12.05	102	Kooyman et al.(1976)
Spheniscus humboldti	3.87	3	.	10.96	9.61	114	Drent and Stonehouse (1971)
Megadyptes antipodes	4.80	1	.	11.54	11.26	98	Stonehouse, in Drent and Stonehouse (1971)
Eudyptes pachyrhynchus	2.60	4	.	6.94	7.18	97	ibid
E. chrysolophus	3.78	5	-	13.4	-	-	Brown (1984)
E. chrysolophus	3.87	4	-	8.6	-	-	Gavrilov (1977)
E. crestatus	2.33	2	-	5.8	-	-	Gavrilov (1977)
E. crestatus	2.51	4	-	10.0	-	-	Brown (1984)
Eydyptula minor	0.90	6	.	4.44	4.08	109	This study

a. Equations of Aschoff and Pohl (1970a):

active (α) $H_{sm} = 4.41M^{0.729}$

rest (ρ) $H_{sm} = 3.56M^{0.734}$

b %Pred = Obs/Pred . 100

uniformly aquatic and thereby share a thermally hostile environment which may confer a common basis for metabolic segregation.

A considerable amount of data on penguin metabolism is available for comparison. However, these measures include a wide range of conditions and experimental techniques and consequently are not all suitable for comparative use. Published values of standard metabolic rate in penguins are given in Table 2.2. Since values excluded from this analysis have been used in the alternative compilations listed above, further discussion on their validity is required.

Most exclusions are due to artificially elevated metabolic rates. Brown (1984), Croxall (1982), Ricklefs and Matthew (1983), and Weathers (1979) cite data for standard metabolism in the white-flippered penguin (Eudyptula albosignata) from Pinshow et al. (1977). This measurement was taken from penguins wearing a mask while standing on a treadmill as part of a locomotion study. Ricklefs and Matthew, and Weathers also included data for gentoo (Pygoscelis papua) and macaroni (Eudyptes chrysolophus) penguins from Scholander (1940). These measurements were not basal but were derived from penguins restrained on a wooden frame during a study of diving physiology. Ricklefs and Matthew (1983) measured metabolic rate in Adelie penguins from a constant volume respirometer. These birds were not acclimatized to the chamber and there is no indication in that resting levels were obtained since measurements of oxygen consumption were summed over a single hour period for each bird tested. A singular addition to Weather's list of penguin species was the basal metabolic rate of a predicted penguin from Pinshow et al. (1977) which equalled 100% of its own predicted level.

Other data were not considered since they were derived from measurements in the field. Outdoor experiments with masks on emperor and king penguins (Le Maho et al. 1976, Le Maho and Despin 1976) were not included in this analysis. Despite the artificial environment afforded by metabolic chambers, they allow more reproducible conditions than the natural environment, and further, correspond with techniques employed for other birds. The data of Le Resche and Boyd (1969) were in addition compromised since no methods or weights were given.

Observed metabolic rates of penguins in Table 2.2 show no consistent difference when compared to the appropriate equations of Aschoff and Pohl (1970a). Since the data of Gavrilov and Brown give no information on diel phase, further comparison may be made by lumping the data into the single predictive equation:

$$H = 4.17\ M^{0.72} \quad (2.4)$$

$$(r = 0.958,\ F_{1,11} = 111.3,\ S^2_{y.x} = 0.064,\ S_b = 0.07)$$

This function is 10% greater than given for non-passerines by Lasiweski and Dawson (1967) in Table 1.1 and intermediate between the equations for active and rest phases given by Aschoff and Pohl. All genera and 12 of the 18 species in the Order Sphenisciformes are represented in this analysis which covers the range of penguin body weights. Hence there is little reason to suggest that penguins can be metabolically distinguished from the general equations for standard metabolic rate in non-passerines.

A potential source of error in the use of such predictive equations is variation in body weight due to energetic reserves (fat and protein) (Tuite 1984). This problem is important in penguins which seasonally accumulate substantial stores of visceral and subcutaneous fat in preparation for breeding and moult fasts. The increase in mass before moult approaches 50% of normal body weight (Stonehouse 1970). Since fat is less metabolically active than other tissues, it may be supposed that lean body weight may better predict metabolism than total body weight. However, there appear to be relatively few studies of metabolism in birds in relation to body condition. Such analyses are complicated by possible changes in basal metabolism in addition to changes in weight since adjustment of lipid reserves in birds is closely associated with season (King 1972).

Penguins appear to differ in metabolic strategy from marine mammals which are reported to have elevated levels of metabolism when compared to their terrestrial counterparts (Irving 1973). Penguins, however, are not exclusively marine and spend considerable periods on land when breeding or moulting. During these periods the birds may be

subject to extensive fasts; and as Weathers (1979) notes, a high metabolic rate at these times would be mal-adaptive.

On the other hand, doubts have recently been expressed about the validity of elevated metabolic levels in aquatic and marine mammals (Dawson and Fanning 1981, Lavigne 1982). Dawson and Fanning argue that high indices of insulation and metabolic rate could cause problems with heat dissipation on land. Restriction of energy expenditure (via heat conservation) would be energetically more economical than an initially high level of heat production.

2.4.4 Conductance

A measure of heat flow from the little penguin at various air a water temperatures in this study was calculated from the expression:

$$\text{Whole-body conductance} = \frac{\text{heat production}}{(T_b - T_a).(\text{surface area})} \quad (2.5)$$

where surface area was determined using the Meeh value of 8.7 found for two little penguins. Mean conductance (± SD) below the thermoneutral zone was thus determined to be 1.93 ± 0.15 W/(m².°C) (n=37). If corrected for the caloric equivalent of evaporative water loss from the equation of Crawford and Lasiewski (1968) and assuming that the latent heat of vaporization of water equals 2.43kJ/g, then an approximate value of dry conductance would be 1.71W/(m².°C).

There are a number of predictive equations by which these values may be compared to those expected for similar-sized nonpasserines. Calder (1974) predicts an overall (wet) conductance for a hypothetical 900 gram nonpasserine as 1.13 W/(m².°C), a value 0.59 times that found in this study. Calder's equation is based on a Meeh value of 10. If it is adjusted to a Meeh value of 8.1 (Walsberg and King 1978) then the prediction becomes 1.66 W/(m².°C) which is still below that presented for the little penguin.

Conversly, the adjusted equation for dry conductance from Calder (1974, equation 1.7) predicts a dry heat transfer coefficient of 1.70

TABLE 2.3
COMPARISON OF OBSERVED AND PREDICTED EXTERNAL SURFACE AREA IN PENGUINS

SPECIES	MASS	SURFACE AREA (cm^2)			REFERENCE
	(kg)	Obs	$Pred_a$	$\%Pred_b$	
Aptenodytes forsteri	16.85	5700	5150	111	Le Maho et al.(1976)
A. forsteri	22.70	6500	6282	104	ibid
A. forsteri	25.15	6800	6727	101	ibid
A. forsteri	26.10	6800	6895	99	ibid
A. forsteri	26.75	6400	7009	91	ibid
Pygoscelis adeliae	2.57	1652	1469	112	Johnson and West (1973)
P. adeliae	3.55	2050	1822	113	Kooyman et al.(1976)
Eudyptes crestatus[c]	3.6	1810	1839	98	Stahel, unpub.
Eudyptula minor	0.94	815	751	109	This study
E. minor	1.05	921	809	114	This study

a. Equation of Walsberg and King (1978a):excluding emperor penguin as $7.81m^{0.667}$

b. %Pred = Obs/Pred . 100

c. Bird found recently dead on Macquarie Island 1981, methods as for *E. minor*

$W/(m^2.°C)$ for a 900g bird, identical to dry conductance calculated for the little penguin. Aschoff (1981) recently presented equations for minimal conductance in birds from metabolic determinations. Aschoff's equation predicts a value of 0.03 ml $O_2/(g.h.°C)$ for a 900 g nonpasserine in its activity phase. Recalculating the data for the little penguin below the thermoneutral zone in these units gives a mean value of 0.032 ± 0.003 $mlO_2/(g.h.°C)$, similar to that expected. From these comparisons it appears that little penguins have similar levels of minimal conductance to flying birds.

2.4.5 Conductance in Sphenisciformes

A priori, the equation for overall conductance given above implies that a relatively low body temperature yet equivalent standard metabolic rates to other birds should confer high values of conductance in penguins. Previously published values for conductance in penguins are far greater than would be expected from their weight and aquatic life style (Barre 1984, Bech 1980, Gavrilov 1977).

Le Maho (1977) and Pinshow et al. (1976) argued that penguins should have a relatively smaller surface area than expected for similar sized birds due to the thermal demands of their (aquatic) environment. If this hypothesis is true, then heat transfer coefficients for penguins would be artificially elevated. Walsberg and King (1978a) derived a general equation for surface area in birds which is compared with data for four species of penguins in Table 2.3. The data for Adelie and emperor penguins are not strictly comparable with that of Walsberg and King since the beak and feet were included in the measurements. This error is probably negligible in allometric comparison. Despite the inequality in the range of body weights considered, there is a close association between observed and predicted surface areas in penguins.

Bech (1980) suggested there may be a minimal level of conductance in large birds. This hypothesis may well reflect the paucity of conductance data at these weights, since predictive equations for thermal conductance are mostly derived for relatively small birds. The maximum body weight in the equation of Aschoff (1981) and Lasiewski et al. (1967) is only 2.4 kg and 2.8 kg in

TABLE 2.4
THERMAL CONDUCTANCE IN PENGUINS

SPECIES	BODY MASS kg	CONDUCTANCE $M/(m^2 °C)$	REFERENCE
Aptenodytes forsteri	24.8	1.31_1	Le Maho et al.(1976)
A. forsteri	23.4	1.57	Pinshow et al.(1976)
A. patagonica	11.08	$1.36_{1,4}$	Gavrilov (1977)
		$(2.02)_3$	
A. patagonica	12.45	1.68_1	Barre (1984)
Spheniscus humboldti	3.87	$1.20_{1,2}$	Drent and Stonehouse (1971)
Eudyptes chrysolophus	3.87	$1.37_{1,4}$	Gavrilov (1977)
		$(2.56)_3$	
E. crestatus	2.33	$1.55_{1,4}$	Gavrilov (1977)
		$(1.27)_3$	
Eudyptula minor	0.90	1.71	This study

(1) at lower critical temperature

(2) recalculated by Le Maho et al.(1976) with adjustment of surface area to that found for other birds

(3) from Table 2 in Gavrilov (1977), units converted from original report, assuming a surface area coefficient of 8.1

(4) calculated as $(M - E)/T_b - T_a)SA$ from Table 2 in Gavrilov (1977) using an estimate of evaporative water loss from Crawford and Lasiewksi (1968) and SA from Walsberg and King (1978a)

Herreid and Kessel's (1967) compilation. Bradley and Deavers (1980) also noted that conductance in mammals above 5 kg appeared to plateau but pointed out that data at these weights were scarce. Spotila and Gates (1975) argue that increasing insulation and body size act to decouple an animal from its environment, and although thick insulation is important to small animals it is relatively less effective in large animals.

It may be argued that a minimal level of conductance in large birds would not confer a major thermal disadvantage since the increment in metabolic heat production with decreasing temperature becomes a smaller fraction of standard metabolism with increasing body weight. In penguins, however, the high cooling capacity of water evokes large increases in heat production (Figure 2.1, Barre 1981, Kooyman et al. 1971, 1976) so that a decreased conductance would be beneficial.

The lack of measurements for large birds makes the use of predictive conductance equations inapplicable for comparison with large penguins. In addition, the conductance data for large birds cited by Bech (1980) and Barre (1984) (both from the compilation of Drent and Stonehouse 1971) may not be relevant to general analysis. The data of Benedict and Lee (1937) refer to geese housed indoors and were calculated from the increases in heat production which varied from 6 to 55% between birds at thermoneutrality and 10°C. The measurement of Romijn and Lokhurst (1966) appears to be derived from a figure describing the metabolic response to cold in a single hen without data in the text. Of interest, Bech's (1980) data for conductance in the mute swan are derived from summer acclimatized birds. Although conductance in winter acclimatized swans is greater than in summer birds above -30°C, it was still decreasing at this temperature.

Minimal values of conductance in penguins are shown in Table 2.4. There is some confusion about Gavrilov's data since it is not clear from his text how conductance values were calculated. Values of body temperature, lower critical temperature, and basal metabolic rate (assuming an approximate evaporative water loss from the equation of Crawford and Lasiewski 1968) from Table 2 in Gavrilov may

be combined to give a single estimate of minimal conductance for each species. The resulting values thus calculated are much lower for the macaroni and king penguins but greater for the rockhopper penguin. I have presented both sets of data in Table 2.4.

Thermal conductance data for penguins in this analysis show considerable scatter. No significant relationship was found between conductance and body mass from the data in Table 2.4 which after logarithmic transformation gives:

$$C_{penguin} = 1.53M^{-0.025} \quad (2.6)$$

($r=-0.23$, $F_{1,17}=0.327$, $p < 0.75$, $S^2_{y.x}=0.0034$, $s_b=0.043$)

The exponent in equation (2.6) does not significantly differ from zero ($t_{1,7}=0.577$, $p < 0.9$). Disparity in experimental procedures, and derived variables in Table 2.4, however, may impose considerable error in this analysis. This is evident in the conductance values for the peruvian penguin (S. humboldti, 1.2 W/(m².°C), Drent and Stonehouse (1971)) and the similar sized royal penguin (E. chrysolophus, 2.6 W/(m².°C), from the text table in Gavrilov (1977)).

On the other hand, the dry heat transfer coefficient in the little penguin (1.71 W/(m².°C)) is similar to that reported for the king penguin (1.68 W/(m².°C)) by Barre (1984) despite a ten-fold difference in size. Comparison between the little penguin and the largest penguin species, the emperor penguin (1.31-1.57 W/(m².°C); Le Maho et al. 1976, Pinshow et al. 1976) also indicate that thermal conductance in penguins does not follow the general scaling relation expected for birds. Conductance in the emperor penguin is expected to be half that of the little penguin from Calder (1974, equation 1.7).

Moreover, conductance values given for other birds are lower than those given for penguins. Woolley and Owen (1977) give the slope of heat production with temperature below the thermoneutral zone in black ducks (1.18 kg) as 0.13 W/°C (units converted from original report). Combined with the equation of Walsberg and King (1978) for surface area an approximate total heat transfer coefficient is 1.45

W/(m°.²C). Gessaman (1972) gives the slope of the metabolic response to cold in the snowy owl (2.1 kg) as 0.13 W/°C which becomes 1.02 W/(m°.²C). Although conductance is likely to be the most plastic parameter in energetic analysis (Drent and Stonehouse 1971), from these values I agree with Pinshow et al. (1976) that conductance in penguins, despite their aquatic environment, is not particularly low compared to cold resistant birds.

2.4.6 Penguin plumage

What explanation may be offered for the relatively high heat transfer coefficients in penguins? The primary resistance to heat loss in birds is the insulation provided by their feathers. The aquatic lifestyle of penguins, however, has meant that their plumage must also function as a waterproof barrier in water. The contour feather of a penguin is a short lanceolate quill with a downy base and a strongly curved shaft. These feathers are densly packed over the body surface without apteria (feather tracts) although brood patches develop annually in the mid-ventral line of the abdomen (Chandler 1916, Pycraft 1907, Schtefan 1977, Watson 1883). Rijke (1970) discusses the water repellancy of penguin plumage in comparison with other birds.

The importance of feathers in maintaining homeothermy in penguins is illustrated by jackass penguins whose insulation was disrupted by coating their feathers in oil. These birds became hypothermic after only 15 minutes immersion at a water temperature of 20°C (Erasmus et al. 1981). Comparison of temperature gradients between the core and skin surface indicate that the plumage and boundary layer of emperor penguins contributed 86% of total insulation in cold air (Le Maho et al. 1976; Jarman 1973). At the lower critical temperature of 10°C the little penguin was found to have a ventral skin temperature of 31°C and core temperature of 38.4°C. Feathers and the associated thermal boundary layer thereby comprised 73% of the total insulation of little penguins at this temperature (cf Section 4.4.2).

The thermal insulation afforded by an animal's coat depends upon air trapped within the hairs or feathers and generally increases with

coat thickness (Cena and Clark 1979, Scholander et al. 1950a). Penguin feathers, however, are small with a mean length of 2.8 ± 0.5 cm within the Spheniscidae (Stonehouse 1967) so that the short lanceolate quills comprise a water-proof barrier upon immersion. As such, effective plumage depth of penguins is limited and their feathers, while essential for insulative integrity in water, nevertheless may allow relatively high rates of heat loss on land. I suggest that the deviation from predicted values in larger penguins is due to their plumage being much smaller in depth than for other birds of similar weight. Gavrilov (1977) independently ascribed a higher rate of thermal conductance in penguins to a relatively shallow coat depth.

Does penguin plumage differ from general relationships for plumage quantity in birds? The quantity of plumage varies with body size in birds (Calder and King 1974, Kendeigh 1970). The relationship between the number of feathers per unit surface area and body weight can be shown (after Kendeigh 1970) as:

$$No./cm^2 = 93.7\ m^{-0.488} \quad (2.7)$$

By contrast penguins have the same number of feathers per cm^2 in both large and small species, (11-12/cm^2, Stonehouse 1970). If this data are compared with the general equation for birds given above, then a hypothetical 1,000 g bird (equal in weight to the little penguin) is predicted to have 4 feathers/cm^2 , and a hypothetical 11,000 g bird (of similar weight to the king penguin) would have only 0.8 feathers/cm^2. However, plumage density of a 11 kg emu was 9.4 feathers/cm^2, similar to that found in penguins (Stahel, unpubl. data). Lowe (1933) found that a young gentoo penguin has the very high density of 48 feathers/cm^2, which indicates that the coat of chicks is again denser than adults.

An indication of the insulative properties of plumage is often given as a first approximation by its weight (Kendeigh 1970). Weight of plumage varies with body weight (from Turcek 1966) as:

$$W\ (grams) = 0.09\ m^{0.95} \quad (2.8)$$

TABLE 2.5
PLUMAGE THICKNESS IN BIRDS

SPECIES	WEIGHT (g)	PLUMAGE THICKNESS (cm)	REFERENCE
Parus atricapillus	11.2	0.93	Hill et al.(1980)
Poephila guttata	11.5	0.35	Porter and Gates (1969)
Emberiza c. citrinella	25.5	0.44	Wallgren (1954)
Richmondena cardenalis	45	0.5	Porter and Gates (1969)
Calidrus melanotos	50	0.86	Chappell (1980)
Phalaropus fulicarius	60	0.88	ibid
Falco sparverius	115	1.02	Hayes and Gessaman (1980)
Buteo jamaicensis	1,145	1.58	ibid
Aquila chrysaetos	4,320	2.63	ibid
Pedioecetes phasianellus	1,000	1.48	Evans and Moen (1975)
Gallus domesticus	2,000	2.5	Wathes and Clark (1981)
Gallus domesticus	1,500	2.0	Hutchinson (1954)
Cereopsis novaehollandae	4,650	2.05	Stahel, unpub.
Dromaius novaehollandae	11,000	3.23	Stahel, unpub.
Struthio camelus	100,00	3.0	Crawford and Schmidt-Nielsen (1967)
PENGUINS			
Eudyptula minor	1,000	0.8	This study
Eudyptes crestatus	2,200	2.0	Stahel, unpub.
Pygoscelis adeliae	5,000	1.8	Kooyman et al.(1976)
P. papua	6,200	2.4	ibid
Aptenodytes forsteri	30,000	1.0	Pinshow and Welch (1980)
A. forsteri	30,000	1.0-1.5	Stonehouse (1970)

Measurements of plumage thickness taken by myself are average results of dorsal and ventral surfaces with a pair of modified machinist calipers.

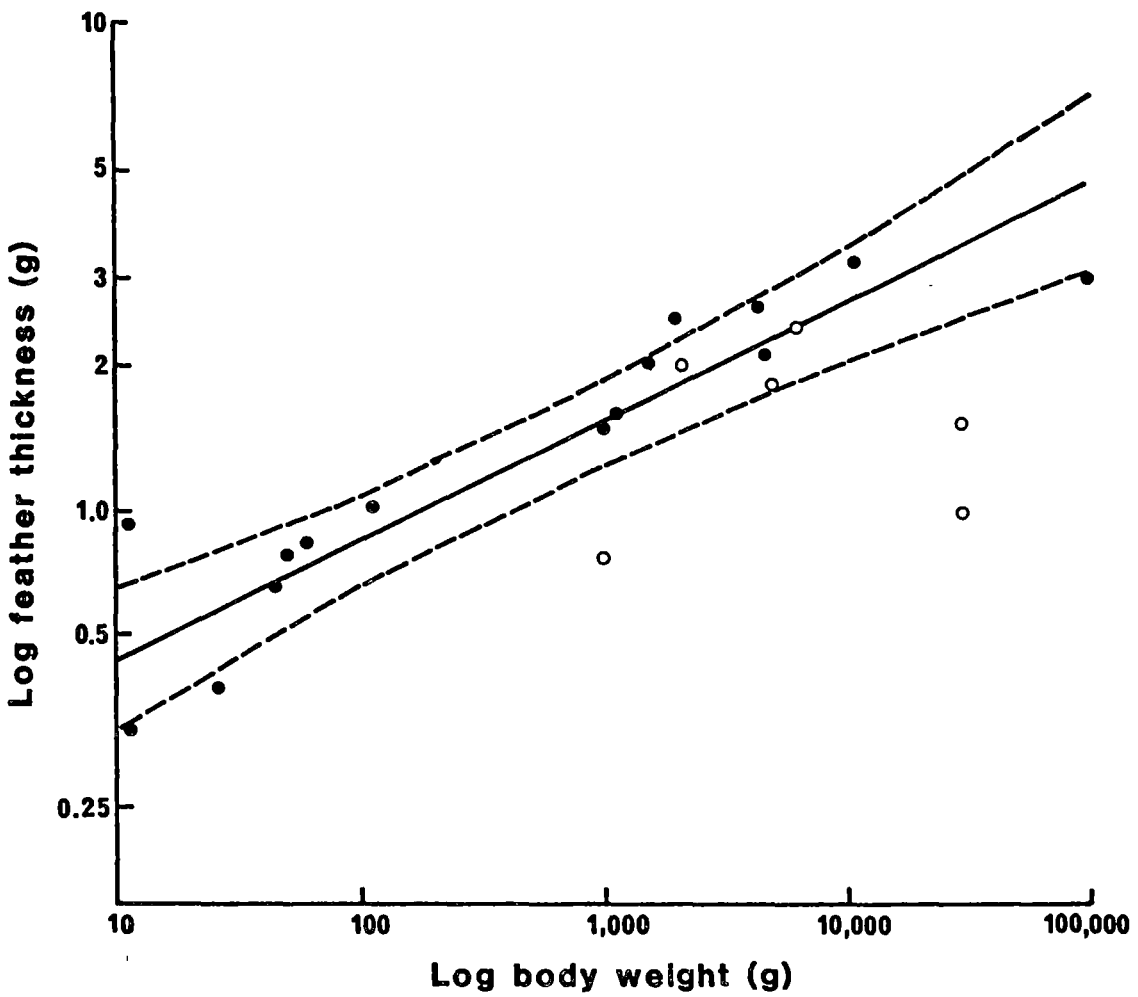

Figure 2.7. Relation of plumage thickness (cm) to body mass (kg) in flying birds (given by solid circles). Solid line represents the equation $P=0.29m^{0.24}$. Dashed lines indicate 95% confidence limits. Plumage thickness in penguins (excluded from the regression equation) is represented by open circles.

How do penguins compare? Turcek (1966) noted that the two penguins in his analysis (the white-flippered penguin Eudyptula albosignata and the little penguin E. minor) had strikingly low values of plumage weight in comparison to birds of similar size. Groscolas (1978) found that the weight of moulted feathers in two emperor penguins was 900 g which, assuming a body weight of 30 kg (Stonehouse 1975) is only 56% of that predicted from equation (2.8). A similar approach by Cooper (1978) gives the weight of dropped feathers of a jackass penguin as 150 g which using a mean body weight of 3 kg is 83% of that predicted above.

Although the weight of feathers in penguin plumage is lower than predicted, there are a number of difficulties in interpretation. It is not clear from Turcek's paper whether flight feathers were included in his analysis and as the feathers on a penguin's wings are very small these data may not be strictly comparable. Furthermore Turcek's data were obtained from birds less than 4 kg in weight and hence the jackass penguin lies at the extreme of his regression whereas the emperor falls far outside it. The plumage weight of a 30 kg emu is again less than that of the emperor penguin (Stahel unpubl. data). Hence there is a quandry of whether these birds deviate from expected relationships due to their weight (in which case the prediction should be expanded to include that data) or due to specific environmental adaptations. Dawson and Carey (1976) point out that predictions about the quality of insulation in different species from the dry mass alone may err since the structure of the feather (particularly the thickness of the shaft) could vary, affecting absolute mass without modifying thermal resistance.

The greater density of penguin feathers coupled with a relatively low weight infers that their plumage would be of shorter depth than that in similar sized birds. Data for plumage thickness in birds is surprisingly scarce. A collection of plumage depths in birds is given in Table 2.5 and presented on logarithmic coordinates in Figure 2.7. The equation for plumage thickness (P) with body weight in birds (excluding penguins) is:

$$P\ (cm) = 0.29\ m^{0.24} \quad (2.9)$$

($r = 0.906$, $F_{1,13} = 59.6$, $S^2_{y.x} = 0.0198$, $S_b = 0.0314$)

This equation can only be regarded as an approximation due to the range of values at both high and low body weights. When the data for feather thickness in penguins in Table 2.5 are compared with other birds in Figure 2.7, it appears that penguins, as a group, do not differ from the expected relationship. On the other hand, V. Buddenbrock (1937, cited in Precht et al. 1973, p 556) reported that in the tawny owl each cm^2 of the skin has an air volume of 4.7 cm^3 above it whereas in diving birds there is only 0.77 cm^3.

The plumage depths in Table 2.5, however, only indicate the "normal" feather arrangement. A cold-exposed bird fluffs its feathers increasing its plumage depth and insulation. Rautenberg (1980) indicated (unfortunately without details) that the depth of feathers may be increased by 2-2.5 times through ptiloerection. The ptilomotor response in birds from the literature does appear to be approximately 1.5-3 times (Crawford and Schmidt-Nielsen 1967, Hill et al. 1980, Wallgren 1954). This response is beyond the capacity of penguins since an increase in depth of this magnitude would exceed the actual length of the penguin feather.

2.4.7 Body Insulation

One method of circumventing a relatively low coat insulation is to decrease the thermal gradient across the feathers. This is seen in Figure 2.4 where ventral skin temperature in little penguins is shown to decrease by approximately 11°C as air temperature decreased from 25 to -5°C. Low skin temperatures with cold exposure in penguins are common and have been recorded in the Peruvian, Adélie, king and emperor penguins (Barre 1984, Bougaeff, quoted in Le Maho et al. 1976, Drent and Stonehouse 1971, Kooyman et al. 1976). This phenomenon appears to be unusual in comparison with most terrestrial birds in which skin temperatures beneath the plumage remain relatively stable (Dawson and Hudson 1970, Veghte 1964) although Calder and King (1974) suggested that vasoconstriction of feathered skin may be more widespread than previously suggested.

Part of the reason why most birds maintain uniformly high

feathered skin temperatures may be their juxtaposition to shivering muscles. The pectoral muscles which average 15% of body weight in flying birds, provide the major source of power for flight and shivering thermogenesis (Calder and King 1974, Dawson and Carey 1976). By contrast, penguins have hypertrophied supra-coracoideal muscles since the wings produce thrust during both up and down strokes during aquatic locomotion (Clark and Bemis 1979). The supra-coracoideus muscle is approximately 50% of the weight of the pectoralis muscle in little penguins compared to 5-17% in typical flying birds (Mill and Baldwin 1983). It could then be initially suggested that the source of metabolic heat production in penguins would be less concentrated than flying birds, assuming that both sets of muscles contribute to shivering thermogenesis. In contradiction to this argument is the observation that ventral feathered skin temperatures of birds still remain relatively high (eg Helfmann et al. 1981). Low skin temperatures in penguins must then be the result of subcutaneous fat deposits and adjustment in peripheral blood flow (cf Section 4.4.2).

Concomitant with low skin temperatures in the little penguin a decrease in the temperature of the peripheral shell was observed, shown by the decrease in shallow cloacal temperatures with decreasing ambient temperature (Figure 2.2). Furthermore, the decrease in both 3 cm and 5 cm cloacal temperatures in water implies that the size of the peripheral shell is increased upon immersion; a result of the greater thermal load faced by the little penguin in water. Unfortunately experiments with labelled microspheres to quantify the degree of alteration in thermoregulatory vascular control in the little penguin were unsuccesful due to difficulties with catheter implantation.

Heat was also conserved by peripheral heterothermy, whereby the temperature of the extremities was allowed to approach that of the environment (see Figure 2.4). This function is mediated by peripheral vasoconstriction and arterio-venous heat exchange in the wings and feet (Frost et al. 1975, Johansen and Bech 1983, Le Maho 1977). Interestingly, Midtgard (1981) found arterio-venous associations in the leg of penguins to be relatively simple in comparison to many birds. However, in addition to vascular adaptations, heat exchange in a vasoconstricted appendage may occur by conduction between blood

vessels and adjacent tissues (Edwards and Burton 1960, Johansen and Millard 1973). The rheological properties of penguin blood may also act to restrict heat loss at low temperatures. Penguin blood has a relatively high apparent viscosity at low temperatures due to high plasma protein concentration and large erythrocyte size (Block and Murrish 1974) which restricts peripheral blood flow in the cold. Penguin blood also has a low yield shear stress which prevents blood stasis and consequent freezing at very low blood flow (Gaurd and Murrish 1975).

My argument that heat loss in penguins is equal to or greater than expected when compared to similar sized terrestrial birds contradicts the traditional view that penguins are over-insulated for life on land (Frost et al. 1976, Stonehouse 1967). Although the little penguin has little capacity to withstand heat exposure, this response is due to a reduced capacity for evaporative water loss. Little penguins in this study increased their respiratory frequency as measured by a pressure transducer attached to the chamber from 8.4 $\pm$ 2.9 (SD) breaths/min (n=31) within the thermoneutral zone to only 30.2 $\pm$ 7.2 (SD) at 35°C despite large increases in heat production and body temperature (cf section 3.4.3 for further discussion). Baudinette, O'Driscoll, and Gill (unpubl. manuscript) have recently confirmed that little penguins only dissipate 40-50% from total heat production from evaporation at high air temperatures.

2.4.8 Heat loss in air and water

The simple linear model of heat transfer in equation (2.5) represents an estimate of the various modes of heat transfer. Total conductance, however, comprises heat transfer between the body core and the animal's surface (internal conductance, k_1) and heat transfer from the surface to the environment (external conductance, k_2) (Gates 1980, Tracy 1972). In steady-state conditions, heat flux from the core to the surface equals that from the surface to the environment. Series conductances can be expressed as:

$$H - E = k_1(T_b - T_s) \quad (2.10)$$

$$H - E = k_2(T_s - T_a) \quad (2.11)$$

where H - E is dry heat loss (W/m^2), T_s is mean surface temperature, and T_a is environmental temperature. Hence (from Tracy 1972):

$$H - E = k_1k_2/(k_1 + k_2)\ (T_b - T_a) \qquad (2.12)$$

I shall apply this model of heat loss to the little penguin in air and water for explanation of the thermal consequences of immersion. Direct measurement of mean surface temperature is difficult. However in a metabolic chamber T_s is relatively constant (Gates 1980). Morhardt and Gates (1974) suggested that the energy budget equation specifying heat transfer between an animal and its environment may be solved in terms of T_s. The energy budget equation, after Porter and Gates (1969) is:

$$H + Q_{abs} = \varepsilon\sigma T_s^4 + h_c(T_s - T_a) + E + C_d + W + S \qquad (2.13)$$

where H is metabolic heat production; Q_{abs} is absorbed radiant energy; ε is surface emissivity; σ is the Stefan-Boltzmann constant; h_c is the convective heat transfer coefficient ($W/(m^2.°C)$). E is evaporative heat loss, C_d is conductive heat loss or gain, W is work, and S is heat storage (W/m^2).

For an animal in a steady-state in a metabolic chamber, the energy budget equation may be simplified by ignoring work and heat storage terms. Conductive heat transfer is usually regarded as minimal since the area of the body in contact with the chamber floor is relatively small. Total evaporative water loss in air was calculated from data for little penguins by Baudinette, Gill, and O'Driscoll (unpubl. manuscript).

Incident radiation is only long wave and can be represented in terms of chamber wall temperature as a function of T_{wall}^4. The radiative exchange terms in the energy budget may be expressed in linearized form as net radiative exchange (Campbell 1977, Gates 1980) as:

$$\varepsilon\sigma\ (T_s^4 - T_{wall}^4) = 4\varepsilon\sigma T_{wall}^3(T_s - T_{wall}) \qquad (2.14)$$

If emissivity is assumed to be approximately 1.0 for both penguin and chamber wall, the error from linearizing radiative exchange will be approximately 5% for a temperature difference of 10°C between the surface and environment (Gates 1980).

Convective heat transfer from an object is a complex function of many variables such as size, shape and orientation of the object, the density, viscosity, specific heat and thermal conductivity of the fluid, the velocity of flow, and whether this flow is turbulent or laminar (Gates 1980).

Such analysis is simplified by the use of dimensionless groups which describe heat transfer and fluid properties in objects of similar shape (Gates 1980, Monteith 1973). Primary amongst these is the Nusselt number (Nu) which relates the convective heat transfer coefficient to the characteristic dimension (d) of the object and the thermal conductivity of the fluid (k) as:

$$Nu = h_c.d/k \quad (2.15)$$

The Nusselt number can be further expressed as the function of other dimensionless groups: the Grashof number (Gr) and Prandtl number (Pr) for free convection, and as a function of the Reynolds number (Re) and Prandtl number for forced convection.

Is a penguin in the metabolic chamber subject to free or forced convection? Air flow rates through the chamber in air were equivalent to 0.14-0.21 m/s. Monteith (1973) provides estimates for the choice between free and forced convection as obtained by the ratio of buoyancy forces (Gr) to inertial forces (Re) in fluid flow. Such analysis indicates a mixed convective regime so that forced convection was chosen particularly when air speeds greater than 0.1 m/s are usually regarded as forced convection (Gates 1980).

Although Kerslake (1972) points out that the characteristic dimension is arbitrary, its choice is important in that it predicts the magnitude of the predicted heat transfer coefficient. Animals are usually approximated as a simple geometric shape. Perhaps the most convenient choice is a cylinder (Campbell 1977) although Mitchell

TABLE 2.6
PHYSICAL PARAMETERS OF WATER, NON-DIMENSIONAL HEAT TRANSFER COEFFICIENTS AND CONVECTIVE HEAT TRANSFER COEFFICIENTS FOR LITTLE PENGUINS IN WATER

Temp. (°C)	Kinematic viscosity $\nu \times 10^3$ (m^2/s)	Re	Pr	Nu	Thermal conductivity ($W/(m^oC)$)	h ($W/m^2 °C$)
0	1.787	1.679	13.7	72.9	0.552	402.2
5	1.514	1.982	11.6	74.8	0.562	420.3
10	1.304	2.300	9.55	75.2	0.574	431.5
15	1.138	2.646	8.03	75.8	0.588	445.9
20	1.004	2.989	6.82	76.0	0.600	456.4
25	0.894	3.358	5.89	76.5	0.611	467.3
30	0.802	3.742	5.13	77.0	0.621	477.8
35	0.705	4.256	4.52	78.6	0.630	494.9
40	0.657	4.566	4.32	80.3	0.628	504.1

Kinematic viscosity calculated from the density and dynamic viscosity of water in Kaye and Laby (1972) and Weast and Astle (1983). Prandtl numbers and thermal conductivity of water with temperature derived from Kreith (1965), Reynolds numbers, Nusselt numbers and convective heat transfer coefficient calculated from equations given in text.

(1976) argues that predicted heat transfer coefficients from a sphere are within 20% of empirical results for such diverse shapes as cow, man, lizard, and insect. In either case d should be related the height of the body as seen by the fluid flow. Both approaches give the characteristic dimension of the little penguin as 0.1m.

There are a number of equations which predict convective heat transfer coefficients from geometrical shapes. Monteith (1973) gives the equation for forced convection across a sphere as:

$$Nu = 0.34\ Re^{0.6} \quad (2.16)$$

in which the Reynolds number is defined by:

$$Re = V.d/v \quad (2.17)$$

where V is windspeed (m/s), d is the characteristic dimension (m) and v is the kinematic viscosity (m^2/s). In air Re for little penguins was 1,200 which gives a predicted Nusselt number of 23.54. From equation (2.13), h_c in air becomes 6.03 $W/(m^2.°C)$.

In water the energy budget equation is further simplified since radiative exchange is negligible and evaporative heat transfer may be ignored. Although the penguins were floating quietly in unstirred water, Boutelier et al. (1977) noted that shivering in man in still water was equivalent to a water speed of 0.03 m/s. Under these conditions forced convection is the predominant means of heat loss.

For flow normal to a sphere, the average Nusselt number (assuming uniform heat flux) in these conditions is given by Thomas (1980) as:

$$Nu = 2 + (0.4Re^{0.5} + 0.06Re^{2/3})Pr^{0.4} \quad (2.18)$$

However, the physical properties of water change with temperature so that an overall estimate of h_c is not valid. The physical parameters of water at different temperatures used to solve the above equation and to calculate the convective heat transfer coefficient are given in Table 2.6.

As might be expected (Mitchell 1974), the predicted convective heat transfer coefficient in water for the little penguin is two orders of magnitude greater than that in air. Empirical results derived from fish models (of similar size to the little penguin but with different shape) give a substantially higher heat transfer coefficient of approximately 1,000 W/(m^2.°C) (Erskine and Spotila 1977).

The penguins in this study were floating at the the surface and thereby not fully immersed. The volume of a one kg little penguin was calculated by displacement to be approximately 1.3 litres. Hence an estimated 25% of the penguins surface area is above the water and exchanges heat with its environment according to the convective and radiative heat transfer coefficients in air. Due to the large thermal sink represented by water the error in predicting T_s by ignoring this fraction is minor.

Conductive heat transfer also assumes more importance in water. Conduction is described for steady-state conditions from a plane surface from Thomas (1980) as:

$$C_d = k/L\ (T_1 - T_2) \quad (2.19)$$

Given the thermal conductivity of water (k) at 20°C from Table 2.6 (0.6 W/(m.°C)) and a characteristic length (L) of 0.4 m (length of a little penguin, Stonehouse 1967) then the conductive heat transfer coefficient is approximately 1.5 W/(m^2.°C) which is small compared compared to the convective heat transfer coefficient at this temperature (456 W/(m^2.°C)) and is ignored in this analysis.

Since convective heat transfer is the predominant means of heat loss in water predicted mean surface temperature in water can then be simply calculated from:

$$H\ (\text{Watts/m}^2) = h_c(T_s - T_w) \quad (2.20)$$

where T_w is water temperature. Heat storage, however, was found to be negative for the little penguin in water as shown by the decrease in

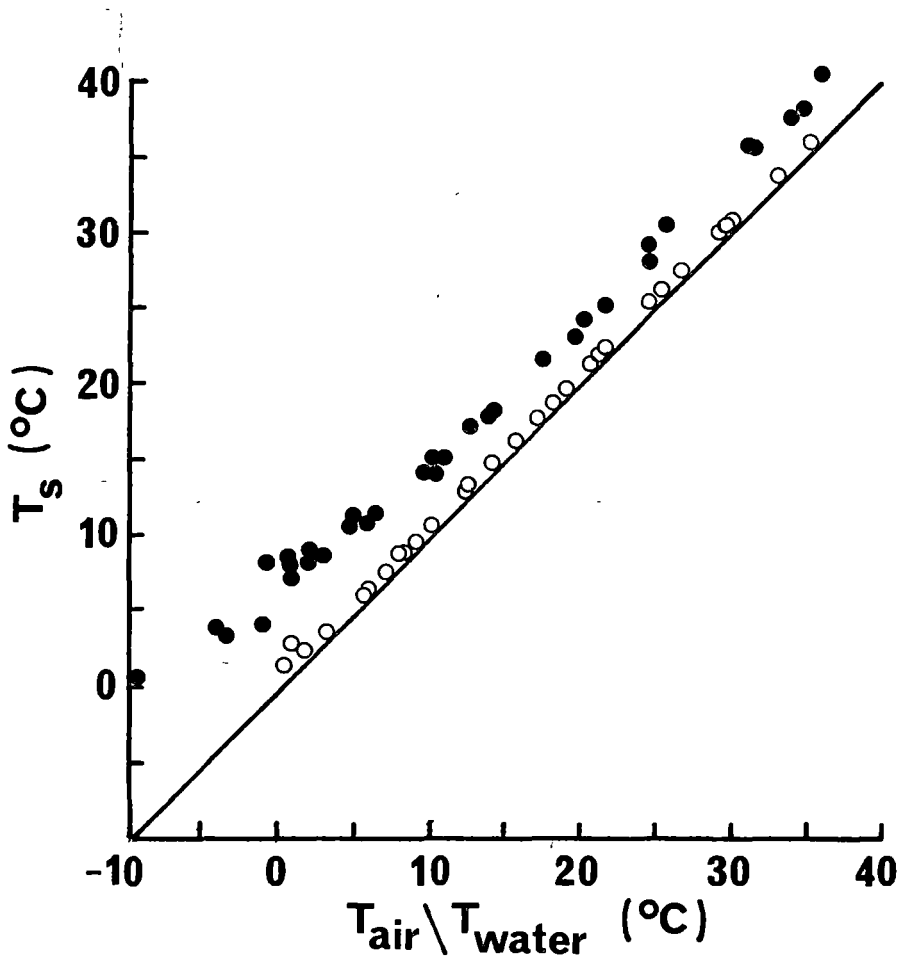

Figure 2.8. Predicted average surface temperatures of little penguins as a function of air and water temperatures. Solid circles: air; open circles: water.

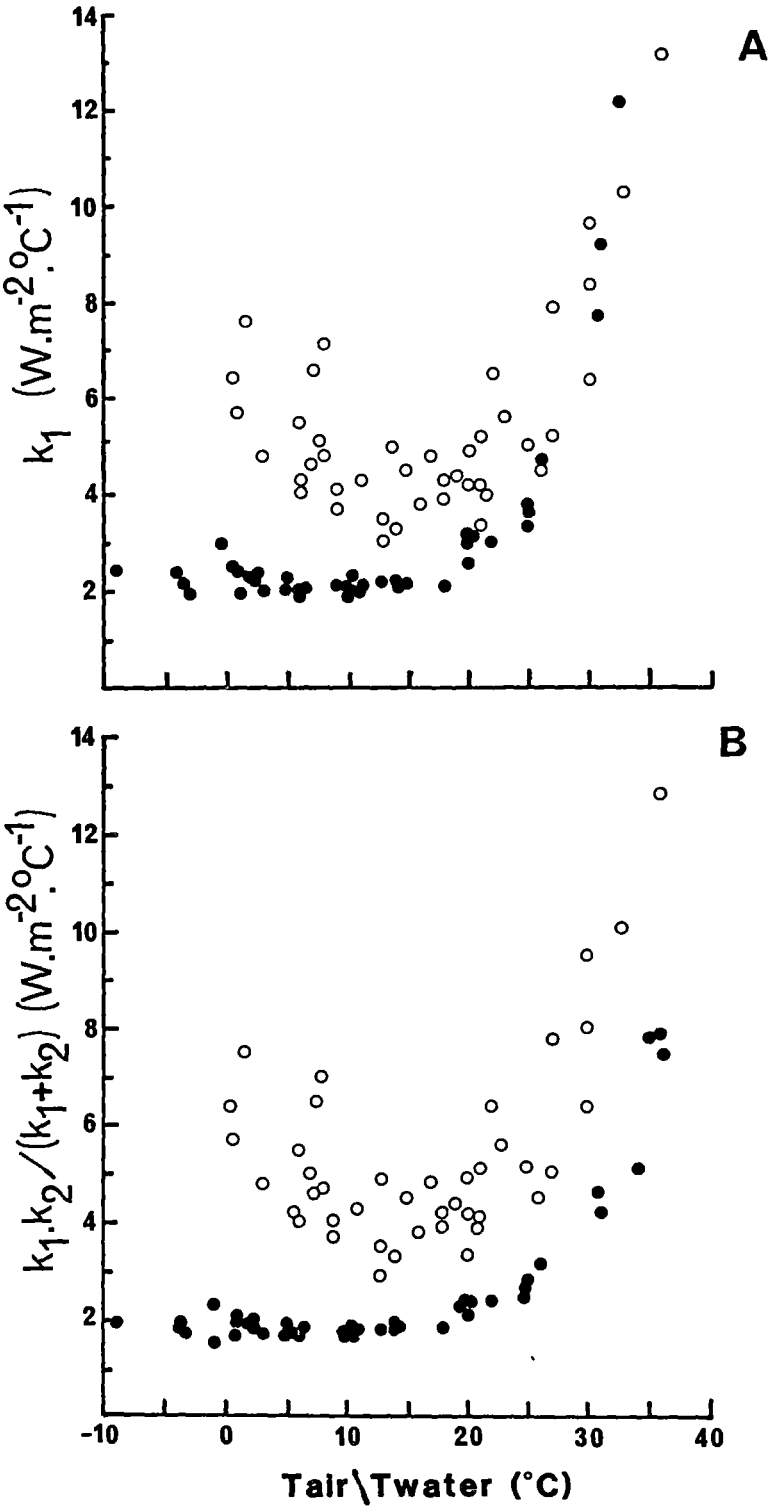

Figure 2.9 A,B. Relation of thermal conductance in little penguins to air and water temperature. A Internal conductance (k_1, W/(m².°C); B total conductance ($k_1.k_2/(k_1 + k_2)$, W/(m².°C)). Solid circles: air; open circles: water.

cloacal temperatures with decreasing water temperatures (Figure 2.2). Although this can be ignored when the penguin had reached equilibrium, at water temperatures below 5°C, body temperature continued to decrease. This heat debt may be expressed as:

$$S\ (J) = W.c.\Delta T_b \quad (2.21)$$

where W equals the weight of a little penguin (1 kg), c is the average specific heat of the body (approximately 3.35 J/(g.°C), Schmidt-Nielsen 1975), and ΔT_b is the change in average body temperature (°C). Given an (extreme) fall in body temperature of approximately 5°C (Figure 2.6), then the calculated heat debt was 16.75 kJ. Since this decrease was over 150 minutes it can be calculated to be equivalent to 21.4 W/m². However, when this component is added to metabolism (251 W/m²) in equation (2.18) the difference in predicted surface temperature is only 0.05°C.

Predicted surface temperatures in little penguins as a function of equations (2.13) and (2.20) are linearly related to environmental temperature as shown in Figure 2.8 with surface temperatures in water remaining very close to water temperature. Internal (k_1) and total conductances ($k_1k_2/(k_1+k_2)$) calculated from predicted surface temperature and equations (2.10) and (2.11) are shown in Figure 2.9. External conductance in air in this analysis ranged from approximately 9 to 12 W/(m².°C), a value greater than h_c in air due to the addition of the radiative heat transfer coefficient. In water external conductance was similar to the convection coefficients given in Table 2.5. The ratio of internal to external conductance (k_2/k_1) is known as the Biot number. Tracy (1972) notes that when this ratio is 10 or greater, overall conductance may be approximated by internal conductance k_1. In air the Biot number ranged from approximately 1 to 6, whereas in water this ratio was 30 to 70.

Despite the difference in Biot numbers between air and water, the values of internal conductance show the same pattern with temperature as overall conductance. In air the mean overall conductance below the thermoneutral zone was 1.82 ± 0.18 W/(m².°C), slightly higher than the value for dry conductance calculated from the conventional formula in equation (2.5).

In water internal conductance shows a parabolic distribution with temperature. The minimum level of conductance between water temperatures of 10 and 20°C was 4.11 ± 0.62 W/(m².°C), 2.3 times that found in air below the thermoneutral zone. As this difference relates to internal conductance, it must be primarily due to responses of the little penguin rather than the disparity between the physical properties of air and water evident in external conductance. Kooyman et al. (1976) showed that conductance in Adelie and gentoo penguin pelts increased by 1.1-1.9 times upon immersion. This difference in the little penguin would have been accentuated since minimal conductance in air included the contribution of ptiloerected feathers rather than a pelt with "normal" feather arrangement. In addition, Kooyman et al. argued that the increase in plumage conductance upon diving and immersion in live birds is greater than seen in pelts due to compression of the feathers to retain water-proofing.

Above water temperatures of 20°C my analysis shows that internal conductance in little penguins increased at approximately the same rate as found at higher air temperatures despite the observation that little penguins required an increased level of metabolic heat production to maintain homeothermy at these temperatures. This change in internal conductance was likely to be almost exclusively the result of peripheral vasomotor changes in blood flow. Feather erection is not possible in water and there is little opportunity for changes in body posture affecting surface area. The similar proportional change in internal conductance at higher air and water temperatures suggests that vasoconstriction was directly proportional to temperature rather than heat flux.

Conversly at water temperatures below 10°C, my results show a paradoxical increase in internal conductance associated with the disproportionate increase in metabolic heat production at these water temperatures in Figure 2.1. It is difficult to partition the increase in metabolism from the increase in internal conductance since conductance incorporates heat production in its solution.

The rapid increase in metabolism at water temperatures below

10°C in the little penguin may have been mediated by the decrease in body temperature at these conditions (Figure 2.6). In man immersed in water, shivering thermogenesis is reported to increase in association with stimulation of deep body temperature receptors (Cannon and Keatinge 1960). Similarly, Hammel et al. (1977) noted that hypothermia caused by ice ingestion elevated metabolic rate in the Adelie penguin by 300%. Spealman (1968) argues that shivering in man may prevent body cooling if the environment is not too cold but that it does not completly repay the heat debt incurred before and during its onset. This heat debt may explain the decreased core temperature in the little penguin with prolonged immersion at a water temperature of 5°C.

Decreasing body temperature implies that heat loss is greater than heat production. Such increased heat loss at low water temperatures may be due to cold-induced vasodilatation of the extremities to prevent cold damage (Kilgore and Schmidt-Nielsen 1975, Murrish and Guard 1977). However, the increase in internal conductance was observed at water temperatures above freezing, although one of the mechanism(s) advanced to explain cold-induced vasodilatation is cold induced paralysis of peripheral blood vessels (Keatinge and Harman 1980, Shepherd and Vanhoutte 1981). Reite et al. (1977) reported that activity of peripheral vascular smooth muscle in the web of duck feet was minimal at temperatures below 8°C. This argument is attractive in that little penguins do not normally encounter environmental water temperatures below 10°C although excessive cold-induced vasodilatation was not observed at temperatures well below freezing in air (Figure 2.4).

Another explanation for the increase in conductance at low water temperatures may be derived from limits to the effectiveness of insulation. Although blood flow to the extremities may reach and be maintained at very low levels, there must be limits to the maximum degree of vasoconstriction within the body. Any heat appearing at the surface of the penguin is rapidly lost to the surrounding water. Once a maximal level of body insulation has been attained, lower water temperatures will result in a disproportionate increase in metabolism.

The importance of the thermal gradient between the penguin and water can be illustrated from equation (2.20) describing heat transfer in water. Combining the convective heat transfer coefficient in water at 10°C (431.5 W/(m².°C)) with the surface area of a little penguin (0.087 m²) gives:

$$H \text{ (Watts)} = 37.5 (T_S - T_W) \quad (2.22)$$

Hence an increase of only 0.1°C in the thermal gradient between surface temperature and water temperature due to vasodilatory blood flow or a limit to the extent of the thermal gradient between the core and skin will require an extra 3.75 Watts (or 84% of standard metabolic rate in air) to maintain homeothermy.

The limit of survival at these water temperatures for the little penguin will then be related to the maximal rate of heat production required to maintain body temperature. From Figure 2.6, it can be seen that a water temperature of 5°C would result in incipient hypothermia. At this temperature equation (2.3) describing heat production in water predicts a metabolic rate of 16.3 W/kg so that summit metabolism was approximately 3.3 times standard metabolic rate in the little penguin.

2.4.8 Limits to distribution

Although the little penguin cannot withstand cold water temperatures, the sea temperatures around Tasmania are relatively constant. Surface temperatures near the colony from which these penguins were collected had an annual variation of approximately 4°C between 12 and 16°C over a seven year period (Rochford 1975). The metabolic cost for homeothermy at these temperatures is not extravagant as resting little penguins would be producing 1.6 to 1.7 times the basal metabolic rate in air at the highest and lowest water temperatures, respectively.

On a broader scale, the distribution of the four species of penguins comprising the genus Eudyptula is limited to Australia and New Zealand where mean sea temperatures are above 10°C (Stonehouse 1967). It is intriguing that the breakpoint in metabolic heat

production in water below 10°C in this study corresponds to the temperature limits of distribution. This investigation indicates, as suggested by Stonehouse (1970), the relatively large surface area to volume ratio of the little penguin and related species in the genus Eudyptula has limited their southern distribution into colder sub-antarctic waters.

The other physiological limit to survival in the little penguin is its inability to withstand prolonged heat stress. Serventy et al. (1971) note that the little penguin is rare north of the central coast of New South Wales and similar latitudes in Western Australia. Heat stress, however, is never encountered in water since even the temperatures of tropical water necessitate increased metabolism to offset heat loss (Figure 2.1). Moreover, by landing at night and nesting in burrows the penguins would not be subjected to considerable heat loads. Ainley (1977) has noted that diving birds are found in cold, turbid waters with high standing stocks of phytoplankton and high food availability. It appears that ecological rather than physiological constraints have primarily set the northern distribution limits of the little penguin.

2.5 SUMMARY

Metabolic rate and body temperatures were measured across a range of air and water temperatures in the little penguin. The standard metabolic rate in air did not differ from predicted levels. Penguins, as a group, have standard metabolic rates similar to other nonpasserine birds.

Deep body temperature in the little penguin was found to be similar to other penguins and slightly below that found for most birds. Body temperature varied with the site of measurement due to an increase in the size of the peripheral shell upon cold exposure at low air temperatures or in water.

Conductance in the little penguin, a measure of heat loss at low air temperatures was approximately equal to that expected for a similar sized bird. Although penguins may be considered cold adapted due to the thermal consequences of immersion, conductance in penguins as a group appears to be relatively high in comparison with other cold-adapted birds. Comparison of conductance in the little penguin with the emperor penguin, the largest penguin species, shows no scaling function with body weight. Higher rates of heat loss than expected in penguins are argued to result from the relatively shallow insulative layer provided by the penguin's waterproof plumage.

Water represents a severe thermal environment to the little penguin since the potential for heat loss in water is two orders of magnitude greater than in air. Metabolic rate in immersed little penguins was greater than in air and gradually increased with decreasing water temperature until a critical water temperature was reached whereupon heat production increased sharply. Prevention of excessive heat loss in water was due to the plumage of the little penguin and changes in body insulation. The metabolic breakpoint in water temperature in the little penguin appears to be due to cold-induced vasodilatation or limits to the extent of body insulation.

CHAPTER 3.

VENTILATION IN AIR AND WATER

3.1 INTRODUCTION

The avian respiratory system differs profoundly from that of mammals. The respiratory system in birds consists of relatively small lungs which maintain a constant volume and are unidirectionally ventilated by a system of air sacs which act as bellows. The functional unit of gas exchange in birds is the tube-like parabronchus. Gas exchange across the parabronchi in birds is described by a cross-current model which appears to result in more efficient gas exchange than the uniform pool of the mammalian alveolar lung. Reviews of the structure and function of the avian respiratory system are well-covered in a number of recent reviews (Bouverot 1978, Brackenbury 1980, Burger 1980, Duncker 1972,1974, Fedde 1980, Lasiewski 1972, Piiper 1978, Scheid 1979,1982).

Ventilation must meet the varying requirements of respiratory gas exchange and also becomes important in thermoregulation at high and low ambient temperatures. The potential heat loss from the respiratory system may theoretically exceed metabolic heat production at low ambient temperatures (Johansen and Bech 1983), whereas respiratory evaporative heat loss is important in maintaining heat balance at high ambient temperatures (Dawson 1982, Richards 1970). The hyperpnoenic response to heat, however, must be balanced against chemical regulation, since increased ventilation resulting from extreme heat stress may lead to excessive loss of carbon dioxide from the lungs and disruption of acid-base status (Burger 1980, Calder and Schmidt-Nielsen 1968).

Penguins are the most aquatic birds and it may be assumed that their respiratory system is well adapted to cope with their diving lifestyle and the metabolic loads imposed by exercise and thermoregulation in water. The respiratory system of penguins, however, is unusual since penguins, along with emus, have the simplest lung structure of birds as they lack a neopulmic

parabronchial net and gas exchange takes place exclusively through paleopulmic parabronchi (Duncker 1972).

Although a considerable body of information exists on the ventilatory response to heat in birds (eg Burger 1980, Calder and Schmidt-Nielsen 1968, Johansen and Bech 1984), comparitively little information has been published on the ventilatory response to cold exposure (Johansen and Bech 1983). Water represents a large thermal heat sink to the little penguin and results in a greatly enhanced metabolic response (Chapter 2). Comparison of ventilation in air and water gives a wide range of effective cold exposure which would be achieved only at very low air temperatures. Further, little penguins cannot withstand prolonged heat exposure (section 2.3.2). The hyperpnoenic response to heat appeared unusual since there were only moderate increases in respiratory frequency at 35°C despite large increases in heat production and body temperature (section 2.4.7). I therefore examined the ventilatory parameters and ventilatory responses of the little penguin to different temperatures and compared these with those obtained from birds capable of flight.

3.2 METHODS

Ventilation was measured from quiet, unrestrained birds by the barometric method of Drorbaugh and Fenn (1955). In summary, inhalation by a penguin in the metabolic chamber (section 2.2.1) results in an increase in chamber pressure due to warming and saturation of the inspired tidal gas. Pressure changes within the ventilated chamber were measured with a Kyowa PG-10GC pressure transducer and displayed on a Beckman type R dynograph. Pressure change is related to an estimation of tidal volume (V_T, ml BTPS) by the formula:

$$V_T = P_{obs}/P_{cal} \cdot V_{cal} \cdot G_A \quad (3.1)$$

where P_{obs} is the observed positive pressure deflection associated with inhalation, P_{cal} is the pressure deflection associated with injection of a calibration volume (V_{cal}) into the chamber, and G_A is the dimensionless constant:

$$G_A = \frac{T_b(P_B - P_c)}{T_b(P_B - P_c) - T_a(P_B - P_b)} \quad (3.2)$$

where T_b is body temperature (°K), T_a is ambient temperature (°K), P_B is barometric pressure (mm Hg), P_c is chamber water vapour pressure (mm Hg) calculated from wet and dry bulb temperatures with a psychometric chart (Chambers 1970), and P_b is water vapour pressure at body temperature (mm Hg). Respiratory frequency (f, breaths/min) was determined by counting inhalations from the polygraph record.

Measurements of respiratory frequency and tidal volume were made at a range of air (-4-37°C) and water (1-36°C) temperatures. Oxygen consumption was simultaneously measured by the open-circuit system described in section 2.2.1. Body temperature was measured from deep cloacal temperature in air or a discrete measurement of oesophageal temperature at the completion of water experiments.

Measurements of respiratory frequency and tidal volume were derived from quiet birds, as shown by stable recordings of oxygen consumption, over periods of at least three minutes for calculation of minute volume. Expired air temperature was measured in association with respiration in three experiments in air by a 48 SWG thermocouple inserted at the entrance of the nares and glued to the beak.

All measurements represent steady-state conditions except for high air temperatures and low water temperatures where the little penguins were unable to equilibrate. An initial adjustment period of at least one hour was allowed before measurements were taken. Chamber temperature in air was changed in a step-wise fashion with at least one hour allowed for equilibration at each test temperature. Water temperatures were not changed by more than 4°C in each experiment.

The mean body weight of the four birds used in respiration experiments was 1.04 ± 0.11 kg.

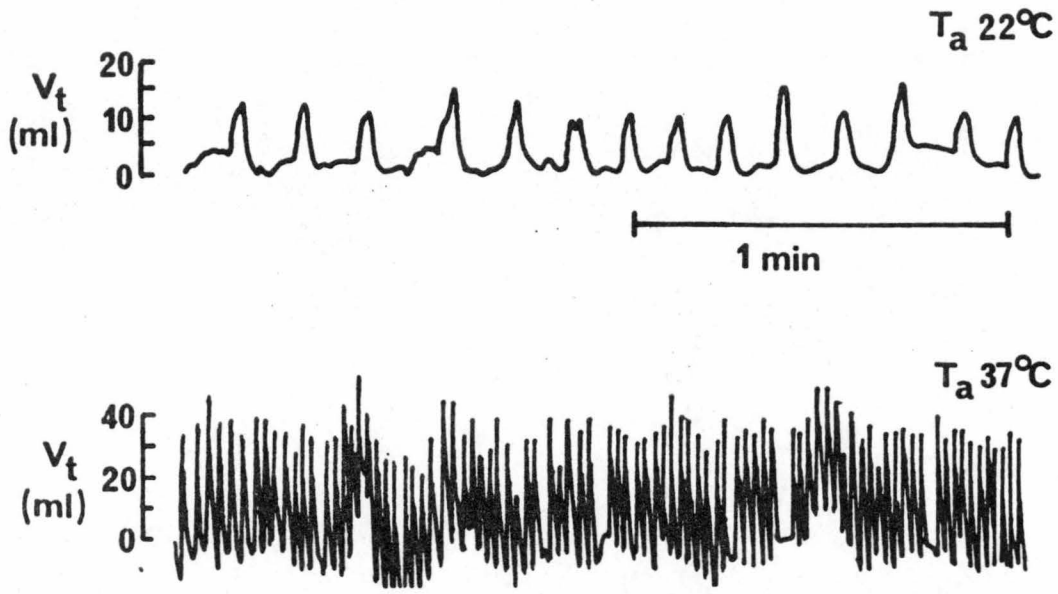

Figure 3.1. Pressure changes produced by a little penguin within a metabolic chamber within a metabolic chamber at thermoneutrality (T_a 22°C), and during extreme heat exposure (T_a 37°C).

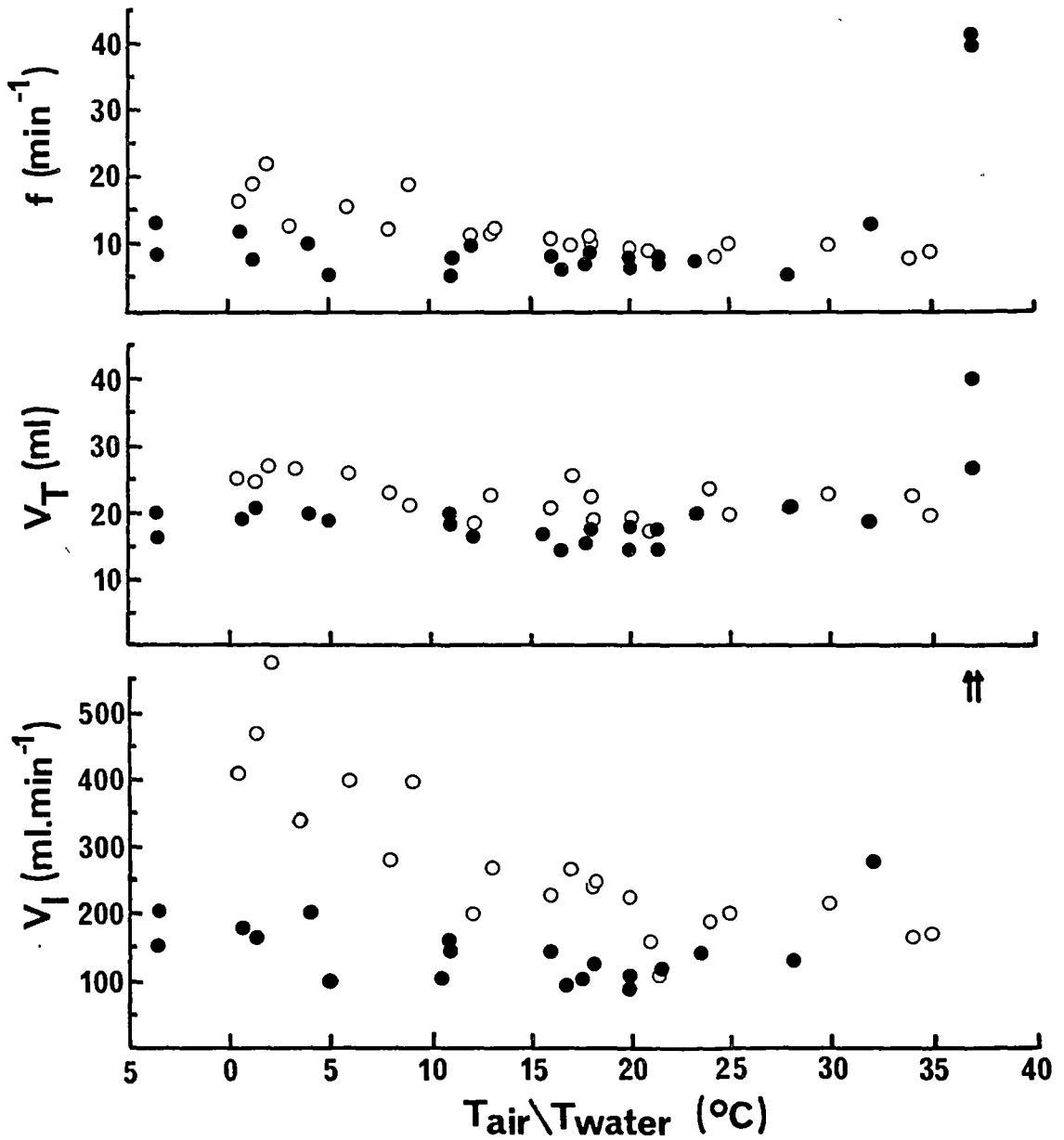

Figure 3.2. Respiratory frequency (f, min^{-1}), tidal volume (V_T, ml), and minute volume (V_I, $ml.min^{-1}$) of resting little penguins at a range of air and water temperatures. Arrows indicate minute volume of heat-stressed little penguins in air (1,143 and 1,644 ml/min). Respiratory volumes expressed at BTPS conditions. Data from four birds with at least two experiments per bird in both air and water. Solid circles:air; open circles: water.

3.3 RESULTS

Representative records of pressure changes associated with respiration in the same experiment for a little penguin at thermoneutrality in air and during heat exposure are shown in Figure 3.1. Respiratory frequency, tidal volume, and minute ventilation of resting little penguins at a range of air and water temperatures are given in Figure 3.2.

Mean respiratory frequency in air at thermoneutrality (10-30°C, section 2.3.1) was 7.1 ± 1.1 breaths/min (n=12). Respiratory frequency increased slightly at lower air temperatures and at the lowest air temperature tested (-4°C) f was approximately 11 breaths/min. At air temperatures above the thermoneutral zone, however, respiratory frequency increased sharply and attained peak values of 40 breaths/min at 37°C. In penguins floating quietly in water breathing rate remained relatively constant at water temperatures above 20°C at 8.4 ± 1.4 breaths/min (n=8). At lower water temperatures respiratory frequency increased with decreasing water temperature until at 1°C it was approximately 18 breaths/min.

Mean tidal volume at air temperatures within thermoneutrality was 17.0 ± 2.6 ml (n=12). The pattern of increased tidal volume with air temperature was similar to that for respiratory frequency since V_T increased slightly at low air temperature and showed a substantial increase at air temperatures above thermoneutrality. Tidal volumes in penguins in water were greater than at equivalent air temperatures below 25°C and increased with decreasing water temperature. Tidal volumes in water experiments above 30°C, in contrast to air, remained relatively constant.

The product of respiratory frequency and tidal volume, inspiratory minute volume (ml/min, BTPS) at thermoneutrality in air was 112 ± 18.7 ml/min (n=12). At temperatures above thermoneutrality in air minute ventilation increased sharply. Values of minute ventilation in two experiments at 37°C were 1,143 and 1,644 ml/min (at chamber water vapour pressures of 7 and 27 mm Hg). Minute

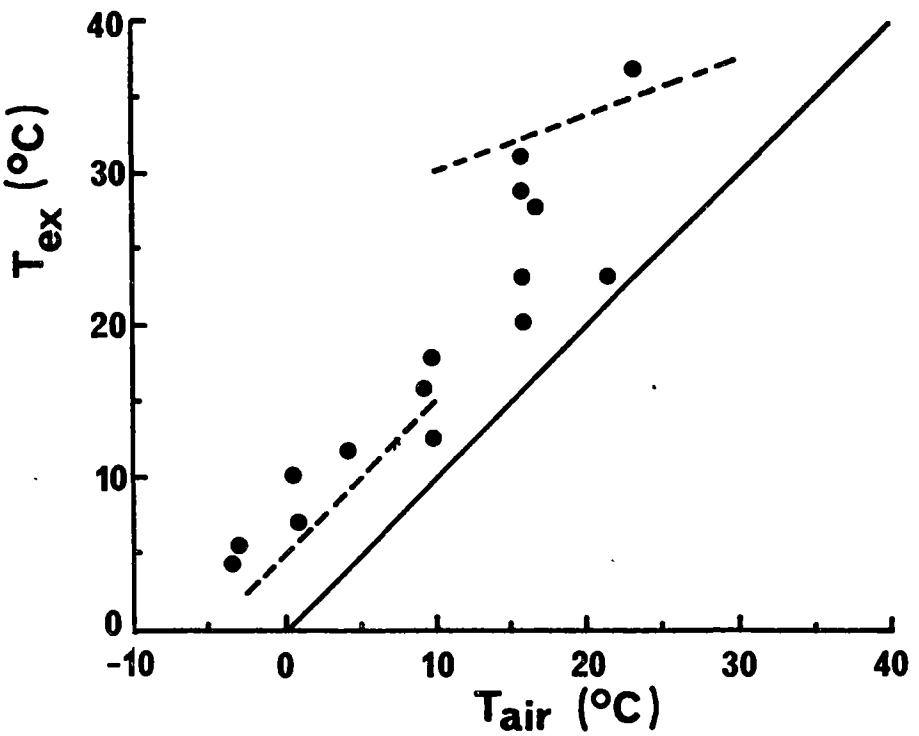

Figure 3.3. Exhaled air temperature (T_{ex}) in the little penguin. Solid line represents $T_{ex} = T_a$. Dashed lines indicate the pattern of exhaled air temperatures in Adelie and gentoo penguins from Murrish (1973).

ventilation in water increased with decreasing water temperature from 170 ml/min at 35°C to approximately 450 ml/min at a water temperature of 1°C.

Expired air temperature (T_{ex}) varied with ambient temperature (Figure 3.3). At low air temperatures T_{ex} was maintained about 7°C above air temperature. Midway through the thermoneutral zone at approximately 15-20°C, however, exhaled air temperature increased sharply to approximately 27°C.

3.4 DISCUSSION

3.4.1 Analysis of the barometric method for tidal volumemeasurements

Tidal volumes calculated from the formula of Drorbaugh and Fenn (equation 3.1) may underestimate true volume since inspired gas should be considered at nasal conditions and cooling and condensation of expired gases may require a longer period than expiration time (Epstein and Epstein 1978, Epstein et al. 1980). Jacky (1980) demonstrated that this error increases as expired air temperature approaches body temperature and as the ratio of inspiratory time (T_I) to total breath duration (T_{TOT}) increases, but typically involves an error of approximately 15-30%. Bucher (1981) notes that a uniform air flow through the respiration chamber, as in this study, gives a constant chamber temperature and relative humidity thereby avoiding problems with baseline drift. In general terms, a small error inherent in the barometric method may be preferable to uncertainties associated with restraint for examination of minimal resting values in comparative studies.

The magnitude of the error in tidal volume due to variations in expired air temperature may be assessed by calculating the volume change from deep body to nasal conditions (G_N). From Jacky (1980):

$$G_N = \frac{T_b(P_B - P_{ex})}{(T_b(P_B - P_{ex}) - T_{ex}(P_B - P_b)} \quad (3.3)$$

where P_{ex} is the water vapour pressure of exhaled air and T_{ex} is the temperature of exhaled air.

The ratio G_A/G_N from equations 3.2 and 3.3 represents the error due to change in volume expansion from air sacs and lung to nasal conditions. This ratio varied with expired air temperature in the little penguin and remained relatively constant at 0.8 below the thermoneutral zone in air but decreased substantially as expired air temperature increased in Figure 3.2 to 0.1 at 23°C. Deep body temperature in respiratory studies is usually assumed to represent

the temperature in the respiratory system (as in this study). However, the capacity of the little penguin to change the size of the body core during cold exposure may affect the temperature in the air sacs. Schmidt-Nielsen et al. (1969) note that temperature of the air sacs in heat-exposed ostriches is 2°C below T_b (associated with respiratory evaporative cooling). Overestimates of respiratory temperature would give lower values of G_A and G_N and hence lower values of tidal volume.

The other potential error in assessing tidal volume from pressure changes is the ratio of inspiratory to total breath duration. This ratio was measured from expanded chart records and was taken as inspiratory breath duration to the beginning of the next breath to allow for cooling and condensation of expired gases. The ratio varied with respiratory frequency as 0.1 at 5 breaths/min to 0.3 at 23 breaths/min.

Corrected tidal volume is given by Jacky (1980) as:

$$V_{Tobs}/V_{Tcor} = 1 - (T_I/T_{TOT})(1 - G_A/G_N) \quad (3.4)$$

Combining concurrent measurements of expired air temperature and respiration gives this ratio as 0.96± 0.029 (n=11). Hence observed tidal volumes lie within 4% of corrected values at temperatures within and below thermoneutrality.

3.4.2 Ventilation in the little penguin

Respiratory parameters in the little penguin may be compared to those predicted for other birds by Lasiewski and Calder (1971). Predicted tidal volume for a hypothetical 1kg bird is 13.2 ml, a value 0.78 times that found for the little penguin in this study. Bech et al. (1979) constructed an expanded allometric equation for tidal volume in birds which predicts tidal volume for a similar sized bird to the little penguin as 16.9 ml, similar to that found in the present study.

Respiratory frequency in the little penguin, however, diverges markedly from expected values. Predicted respiratory frequency from

Lasiewski and Calder is 17.2 breaths/min, 2.4 times that found for resting little penguin at thermoneutrality. Respiratory frequencies in other penguins also appear to be low. Murrish (1982) gives the breathing rate of resting Adélie, chinstrap, and gentoo penguins as 7-8 breaths/min. Kooyman et al. (1973) report that respiratory frequency in emperor penguins immersed in water of -4°C was only 3-4 breaths/min despite vigorous shivering. This latter value is lower than 6 breaths/min reported for the 100kg ostrich (Schmidt-Nielsen et al. 1969) and is similar to that given for resting mute swans at thermoneutrality (Bech and Johansen 1980).

Comparison of minute volume in the little penguin with that predicted by Lasiewski and Calder (1971) is complicated by the uncertainty whether predicted V_I is expressed as SPTD (standard pressure and temperature, dry) or BTPS (body temperature and pressure, saturated). Hence Bucher (1981) compared measured V_I expressed as SPTD with the expected value whereas Bech and Johansen (1980) compared measured V_I at BTPS with the predicted value from Lasiewski and Calder. Since ventilatory parameters reflect the quantity of gas passing through the air sacs and lungs, BTPS conditions should normally prevail. Moreover, predicted V_I from Lasiewski and Calder is based on only six data points, only two of which contain concurrent empirical measurements of V_T and f thereby resulting in inequalities between the equations for V_I and that obtained by multiplying predicted V_T and predicted f. Predicted V_I for a similar sized bird to the little penguin from Lasiewski and Calder is 248 ml/min or 227 ml/min (from multiplying predicted tidal volume and respiratory frequency together). These values are respectively 2.2 and 2.0 times greater than that found in this study for resting little penguins at thermoneutrality in air and result from the low level of respiratory frequency.

Increased minute ventilation in the little penguin with cold and heat exposure was due to both increased rate and depth of breathing. At low air temperatures (-4°C), respiratory frequency increased by 1.5 times the mean value at thermoneutrality whereas tidal volume was similar to thermoneutral values. In water at 1°C, however, tidal volume was 1.5 times the thermoneutral value in air and respiratory

frequency had increased by a factor of 2.5. Bouverot et al. (1976) also reported that both parameters contributed to increased V_I in the pigeon at low ambient temperature. Bucher (1981) found that respiratory frequency provided the major contribution to an increase in V_I in the monk parakeet, whereas increased tidal volume is responsible for increased V_I in the domestic duck, fish crow, kittiwake, and European coot (Bech et al. 1984, Bernstein and Schmidt-Nielsen 1974, Brent et al. 1983, 1984).

Increased ventilation at air temperatures above thermoneutrality in the little penguin was also due to increased breathing frequency and volume. This ventilatory pattern may be described as "simple" panting (Figure 3.1B) (Johansen and Bech 1984). The magnitude of this response in the little penguin was anomalous in comparison to general avian patterns in that tidal volume was enhanced rather than reduced to near the tracheal dead space, and the 5.7 fold increase in breathing rate from resting values at thermoneutrality represents a relatively low frequency response with heat exposure (Richards 1970). The increase in respiratory frequency from resting levels in the little penguin may be compared with the 5-7 fold increase observed during heat exposure in Adélie, chinstrap, and gentoo penguins (Murrish 1982). It is of interest that despite the difference in chamber water vapour pressure at high ambient temperature, the maximum respiratory frequency remained similar, and the greater increase in minute ventilation was derived from V_T.

The increase in minute volume in a little penguin with heat exposure, (10.2 times the resting value at low chamber water vapour pressure) was somewhat greater than a general value of six times normothermic levels in birds (Johansen and Bech 1984). As noted in section 3.4.1, V_T determined from the barometric method may represent a systematic underestimation at higher ambient temperatures which would further increase this response in the little penguin. Absence of any corresponding increase in ventilation in immersed little penguins at equivalent water temperatures implies that peripheral thermoreceptors had little influence on increased ventilation in the little penguin.

Lack of a typical panting response has also been seen in the

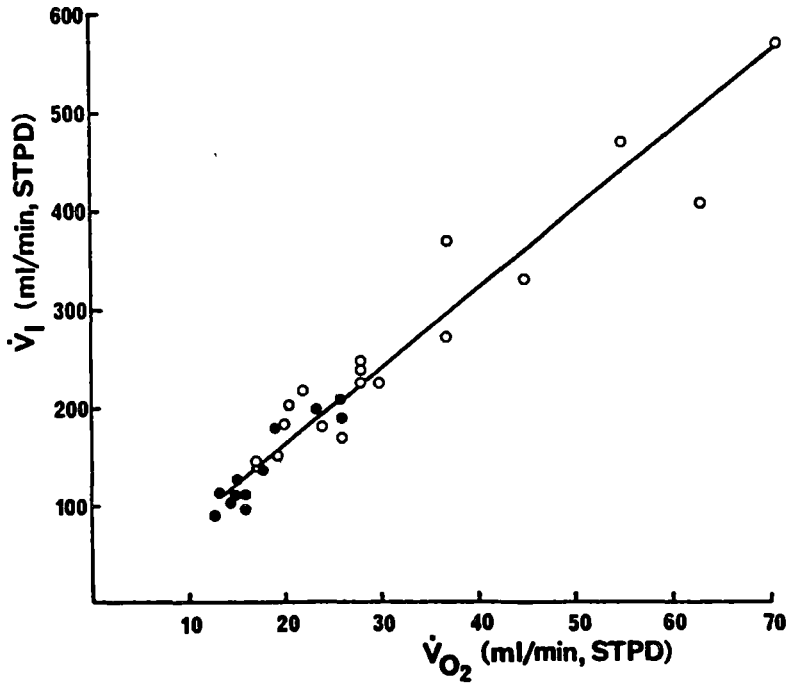

Figure 3.4. Air convection requirement of little penguins in air and water excluding values for heat-stressed penguins in air. The line represents the equation $\dot{V}_{O2} = 7.94\dot{V}_I + 7.52$. Solid circles: air; open circles: water.

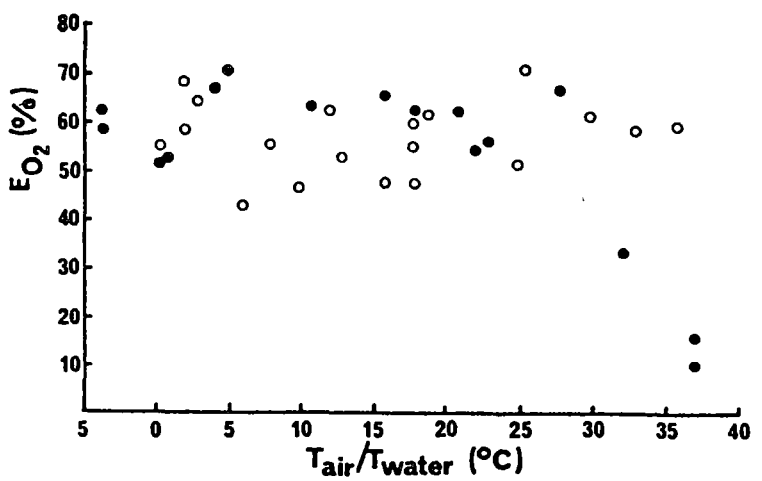

Figure 3.5. Oxygen extraction coefficients of little penguins in air and water from concurrent measurements of minute volume and oxygen consumption. Solid circles: air; open circles: water.

European coot (Brent et al. 1984), although V_T did not increase. This pattern is suggested to be associated with climate or species activity patterns which never suggest hyperthermic conditions (MacMillen 1974, in Brent et al. 1984). Although the climate experienced by little penguins is temperate, the internal heat load generated by swimming could easily be dissipated to the surrounding water. Conversly, the respiratory system of the little penguin is adapted to a diving lifestyle (as discussed below). It is possible that design constraints, associated with this lifestyle preclude an effective panting response although the underlying mechanisms have yet to recieve attention.

The pattern of exhaled air temperature with ambient temperature in the little penguin (Figure 3.3) was similar to that observed in the Adélie and gentoo penguins by Murrish (1973). The breakpoint in exhaled air temperature mid-way through the thermoneutral zone presumably reflects thermoregulatory changes in blood flow to the nasal passages and corresponds with the observed fluctuations in wing and feet temperature at these temperatures (Figure 2.4).

3.4.3 Oxygen extraction and ventilation in the little penguin

The relationship between minute ventilation and oxygen consumption is shown in Figure 3.4 where minute ventilation in air and water (excluding values from penguins in heat exposure) follows the linear relationship:

$$\dot{V}_{O2} = 7.94\dot{V}_I + 7.52 \quad (3.4)$$

$$(r=0.962,\ F_{1,27}=335,\ p<0.001,\ s_b=0.43)$$

where $\dot{V}_{O2}$ is oxygen consumption (ml/min, SPTD) and $\dot{V}_I$ is inspiratory minute volume (ml/min, SPTD). The slope of this equation reflects the air convection requirement or amount of inspired air required to extract one ml of oxygen. These data indicate that increased ventilation in non heat-stressed little penguins remained closely associated with metabolic demands.

Respiration may also be related to oxygen demands by the overall oxygen extraction coefficient (E_{O2}, %) which describes the amount of oxygen extracted from inspired air as:

$$E_{O2} = (\dot{V}_{O2}/F_{IO2}.\dot{V}_I).100 \quad (3.5)$$

where $\dot{V}_{O2}$ is oxygen consumption (ml/min, SPTD), F_{IO2} is the fractional concentration of oxygen in inspired air (0.20946), and $\dot{V}_I$ is inspiratory minute volume (ml/min, SPTD). Values of E_{O2} for little penguins resting quietly in air and water are shown in Figure 3.5. As indicated by the constant value of the air convection requirement, oxygen extraction coefficients remained relatively constant in water and air temperatures below the upper critical temperature with a mean value of 59.0 ± 7.1% (n=29).

My determination of the oxygen extraction coefficient in the little penguin is the highest yet recorded for a bird. Pneumotachographic studies have shown the oxygen extraction coefficient at thermoneutrality as 29% in the duck Anas platyrhynchus (Bech et al. 1984), 20% in the kittiwake Rissa tridactyla (Brent et al. 1983), and 33% in the mute swan (Bech and Johansen 1980). Bucher (1981) reported that barometric determinations of ventilation in the monk parakeet gave a mean oxygen extraction coefficient of 27% at thermoneutrality, with maximum oxygen extraction efficiencies in two experiments of 53% at the lower critical temperature.

Increased oxygen extraction efficencies during cold exposure have been demonstrated in a number of birds: the domestic duck (Bech et al. 1984), the kittiwake (Brent et al. 1983), the European coot (Brent et al. 1984) and the monk parakeet (Bucher 1981). In the domestic duck overall oxygen extraction reaches 41% at -20°C (Bech et al. 1984), whereas in the European coot parabronchial oxygen extraction is 62% at -25°C (Brent et al. 1984). Such reduced ventilatory requirements with cold exposure are explained in terms of heat conservation since the potential heat loss with expired air can theoretically exceed metabolic heat production (Johansen and Bech 1983). In European coots at -25°C, 79% of the heat added to inhaled air was recovered by cooling of expired air over the nasopharyngeal

surfaces, whereas 11% of potential respiratory heat loss was conserved from reduced ventilatory requirements (Brent et al. 1984). Similarly in penguins, Murrish (1973) calculated that 83% of the heat added to inhaled air was recovered during expiration due to low expired air temperatures. The observed reduction in expired air temperature at low ambient temperatures in little penguins in this study (Figure 3.3) indicates that there is a similar curtailement of potential heat loss during cold exposure.

By contrast to the pattern of increased oxygen extraction at low temperatures, oxygen extraction in the little penguin remained conspiciously high at all temperatures in water or in air below the upper critical temperature. The high gas exchange efficiency in the little penguin at thermoneutrality in air implies that the parabronchii in the little penguin were maximally perfused at resting conditions. This level is only attained by other birds in severe cold conditions. The gas exchange efficiency in the little penguin appeared to approach the maximum level available since oxygen extraction did not further increase at low air or water temperatures. The significance of the purely paleopulmic lung to gas exchange in the little penguin (Duncker 1972) is unclear although it is apparent that it does not result in a decreased efficiency.

Since high oxygen extraction was observed at thermoneutrality in this study it does not seem that heat conservation is the major determinant of a reduced ventilatory requirement and, as discussed above, reduced exhaled air temperature is responsible for most of the heat recovered during respiration. Penguins, however, are diving birds characterized by short (20-40s), repetitive dives sustained by aerobic metabolism (Butler and Woakes 1984, Kooyman 1975, Millard et al. 1973). Little penguins have a limited capacity for anaerobic metabolism (Mill and Baldwin 1983) and their small size implies limited total oxygen stores. Observations of little penguins foraging inshore give dive durations of 10-15s (Montague 1983). Lalas (1983) observed mean dive duration of little penguins in Otago, New Zealand to be 24.3s with a mean pause time between dives of 8.9s. Hence a very high oxygen extraction coefficient in the little penguin from this investigation may be explained as allowing rapid replenishment of blood oxygen stores between dives.

At high air temperatures oxygen extraction was decreased as the hyperventilatory response exceeded oxygen uptake. A similar pattern has been shown in the European coot (Brent et al. 1984) and implies a partial bypass of air from the respiratory surfaces. The mechanisms of this response are unclear (Johansen and Bech 1984) although constriction of intrapulmonary smooth muscle has been suggested (Fedde 1980, Salt and Zeuthen 1960).

An altered oxygen extraction coefficient, however, did not enable the little penguin to withstand prolonged heat exposure. The reasons for this are twofold. Despite increased ventilation little penguins only dissipate about 40-50% of total heat production by evaporative water loss at ambient temperatures of 35°C despite signs of severe heat stress (Baudinette, Gill, and O'Driscoll, unpubl. manuscript). Severe "panting" in the Antarctic Adelie, chinstrap, and gentoo penguins results in hypocapnia and severe alkalosis (Murrish 1982) and a similar pattern may be assumed from the large ventilatory increase for the little penguin at high temperatures.

It is apparent, however, that the larger penguin species could withstand somewhat more heat exposure than the little penguin since respiratory frequency increased 3-4 fold for several hours without disruption of the acid-base status (Murrish 1982). This tolerance has been explained by Murrish as the result of an enhanced blood buffering capacity in adult penguin blood and in prolonged heat exposure in penguin chicks by the formation of lactic acid (Murrish 1983). Little penguins, by contrast, appear to have a blood buffering capacity within the normal range for birds since blood bicarbonate concentration was measured as 21 mmol/litre (Stahel and Nicol, unpubl. observation). Baldwin et al. (1984) have recently shown that little penguins have the lowest muscle pH buffering capacity of all penguins so far studied which corresponds with a limited capacity to tolerate lactic acid accumulation and aerobic diving patterns (Mill and Baldwin 1983). Hence the limited tolerance to heat stress in the little penguin in comparison to Antarctic species appears may be associated with an higher susceptibility to respiratory alkalosis.

3.5 SUMMARY

Ventilatory parameters were measured in the little penguin at a range of air and water temperatures. Minute volume at thermoneutrality in air was much less than expected for a similar-sized bird due to a very low respiratory frequency. Cold or heat exposure increased minute volume compared to thermoneutrality due to increased respiratory frequency and tidal volume.

Ventilation in non heat-stressed little penguins remained closely related to metabolic demands. The low minute volume in the little penguin, however, resulted in a very high oxygen extraction coefficient compared to other birds. This high efficiency of gas exchange in the little penguin is suggested to be associated with its short, aerobic diving pattern and to allow rapid replenishment of blood oxygen stores in the short interval between dives.

During heat stress oxygen extraction efficiency in the little penguin decreased although this response did not prevent heat distress. The limited capacity of little penguins to withstand heat exposure appears due to a low level of evaporative water loss and low tolerance of acid-base shifts.

CHAPTER 4.

METABOLIC RATE AND PARTITIONAL INSULATION IN RESPONSE TO WIND

4.1 INTRODUCTION

The dense plumage of penguins provides a major resistance to heat loss during immersion. However, the shallow depth of this water-proof feather layer appears to allow relatively high rates of thermal conductance in air, particularly in large penguins, when compared to other birds (Section 2.4.5/6). This suggestion is mainly derived from measurements in metabolic chambers where environmental conditions are carefully controlled. By contrast, a bird in its natural environment faces a complex interraction of avenues for heat exchange (Porter and Gates 1969). Prominent amongst these is wind which can greatly increase convective heat loss.

The compact nature of penguin plumage has been suggested to confer a high resistance to disorganization and penetration by wind (Le Maho, Dewasmes, and Vu Van Kha 1979, Stonehouse 1967). Hence the effects of wind upon metabolic rate and partitional insulation have been investigated in the little penguin at thermoneutrality and low ambient temperatures to assess the relative importance of internal and external insulative layers in relation to convective cooling.

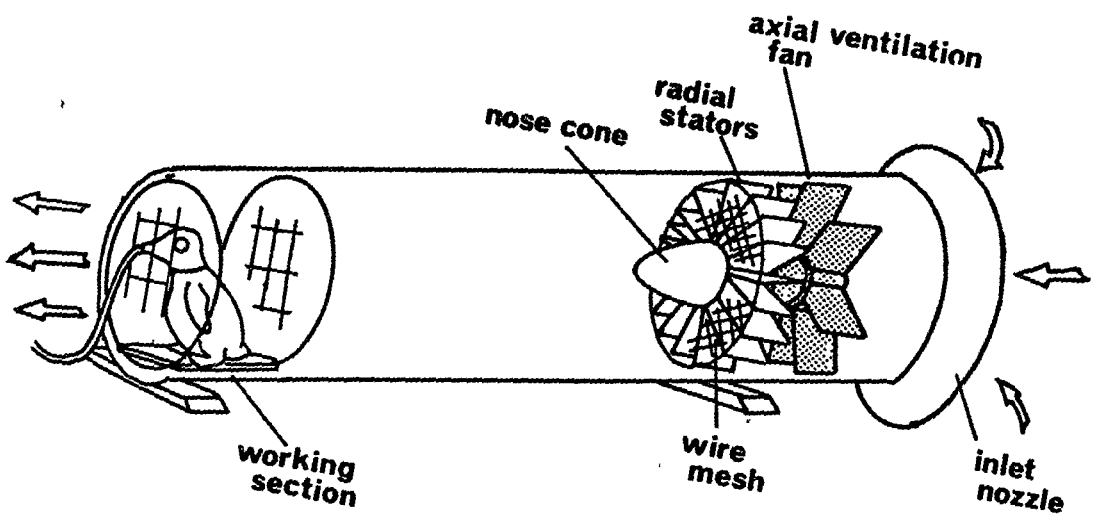

Figure 4.1. Windtunnel used in experiments.

4.2 METHODS

4.2.1 Windtunnel

The windtunnel used in these experiments (Figure 4.1) consisted of an axial ventilation fan (Ziehl-Abegg E350A-4) mounted between circular sections of 0.15 and 1.5 m length and 0.36 m diameter. A car tyre tube was placed on the outside end of the inlet section to give a smooth nozzle profile. Air was forced by the fan across a set of 16 radial stators and nose cone and through a sheet of fine metal gauze to smooth airflow. The working section of the windtunnel was placed at the end of the outlet section to minimize blockage effects and allow easy access to the penguin. This area was 20 cm in length and bounded by grids consisting of thin bars 4 cm apart. The interior of the tunnel was painted matt black to minimize reflected radiation. A small perspex sheet was placed across the bottom of the working section to avoid excessive conductive heat loss to the metal floor of the windtunnel and to expose the penguin to a uniform air velocity. Windspeed was regulated by a variable transformer connected to the fan.

The air velocity profile across the working section was uniform within 10%, as measured by a pitot tube and micromanometer at 4.7 m/s. Mean air velocities (0.8, 1.6, 3.3, and 4.7 m/s) were measured from pressure differences with the micromanometer attached midway along the inlet section. Zero windspeed was taken to be free convection conditions (0.1 m/s).

4.2.2 Metabolic rate and temperature

Metabolic rate was measured with an open circuit system. Air (3.1 - 6.4 l/min) was drawn through a light-weight mask constructed from vinyl plastic and latex rubber with a Thomas compressor. Sample air passed through a mixing chamber, drying tube (calcium chloride) and Brooks flowmeter to an Applied Electrochemistry S3A oxygen analyzer. Oxygen consumption was calculated from equation 3(a) of Withers (1977) assuming a RQ of 0.73 (Section 2.2.1). This system was tested for leaks by passing nitrogen through the system under similar

flow conditions to those in experiments and monitering the appropriate dilution. The output from the oxygen analyzer was displayed on a Rikadenki recorder with 1% full scale deflection.

Body temperature was measured from ingested radiotransmitters (Austec Electronics model UL81T) the output of which was recorded with a stopwatch as time/100 pulses. In a second series of experiments feathered skin temperature was measured with a 38 SWG thermocouple glued to the skin on the sternum. This was led out of the plumage a few centimetres from the measurement site to avoid disrupting the feather layer. Wing temperature was measured from a thermocouple taped at the distal end of the humerus. Temperature was displayed on an Analog Devices digital thermometer calibrated against a thermometer traceable to a National standard. Surface temperatures were recorded with a Barnes 14-220D-1 Instatherm non contact thermometer held horizontally at a distance of 15 cm from the body of the penguin. The non-contact thermometer was corrected for background radiation by the method of Fuchs and Tanner (1966). Wall temperatures were within 0.1°C of ambient temperature at thermoneutrality and 0.4°C of ambient at cool temperatures. The same equilibration times were used as in metabolic experiments.

4.2.3 Experimental procedure

The windtunnel was placed in a constant-temperature room maintained either at thermoneutral (22.1 ± 2.0°C) or cold (6.0 ± 1.4°C) conditions. Ambient temperature was measured by a thermocouple placed in the middle of the leading edge of the working section. The penguin was placed in the windtunnel at least one hour at thermoneutrality before data was collected. In cold conditions this period of time was increased to two hours. A period of one hour was also allowed after each change in windspeed. Windspeed was changed in a random pattern. Metabolic records were considered acceptable for analysis if they showed less than 3% variation for periods more than 15 minutes after each equilibration time. Mean body weight of the four penguins used in windtunnel experiments was 0.89 ± 0.05 kg. By contrast body weight of the single moulting penguin studied was 1.31 kg.

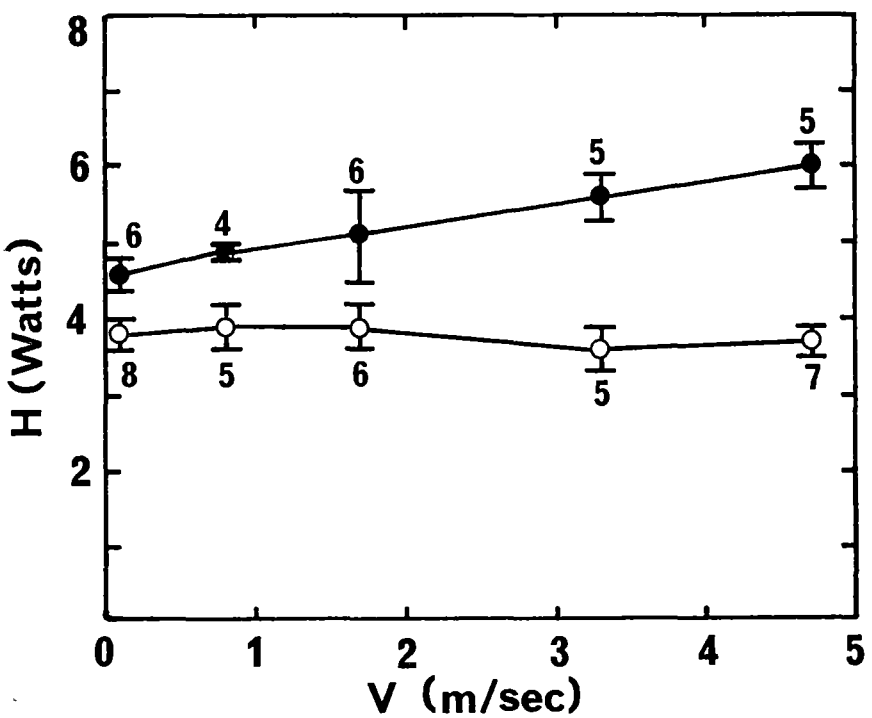

Figure 4.2. Metabolic rate in relation to windspeed in the little penguin at thermoneutral and cold temperatures. Results from three birds with at least two experiments per bird at both thermoneutrality and in the cold. Standard deviations are shown by vertical lines. Numbers above and below each point represent sample sizes. Open circles: thermoneutrality (22°C); Closed circles: cold temperature (6°C).

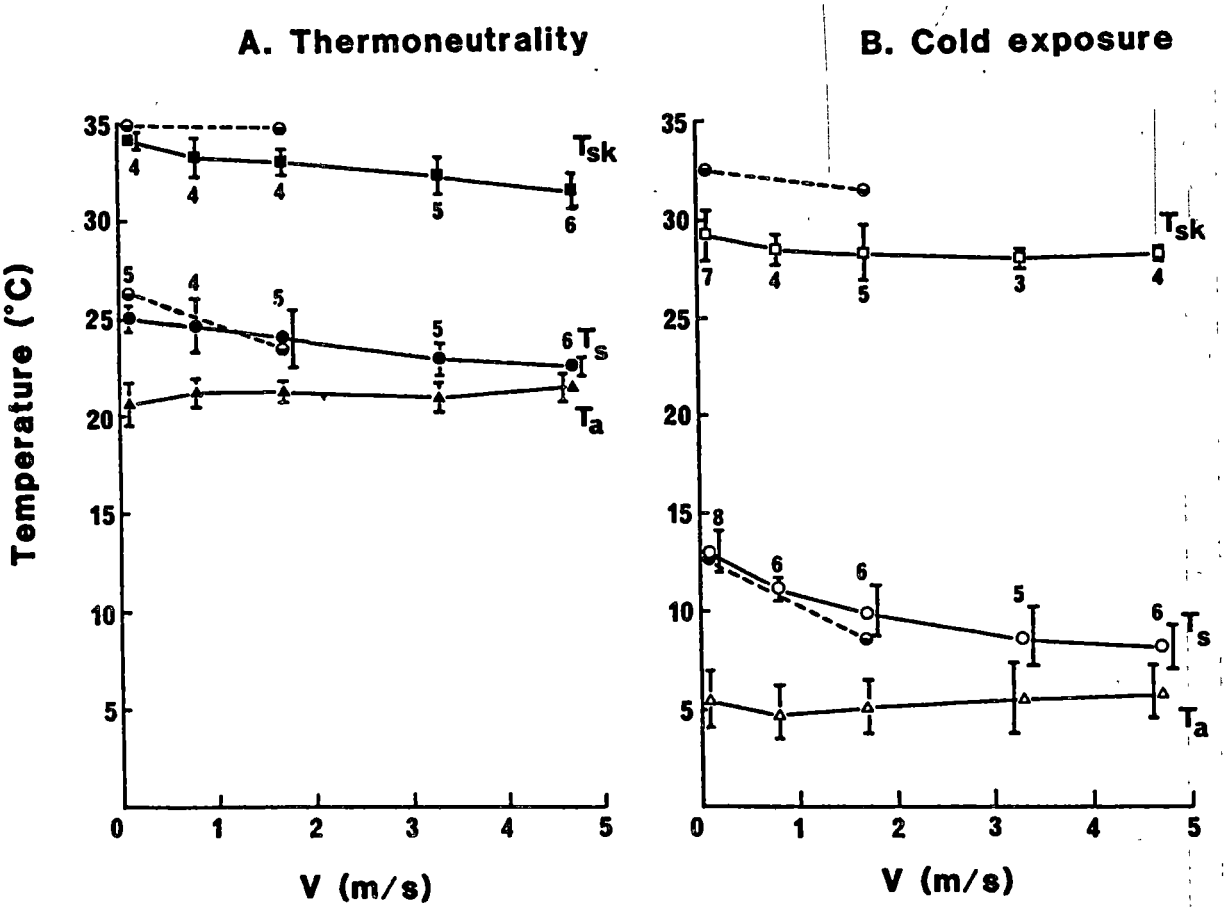

Figure 4.3 A,B. Temperature gradients in little penguins with windspeed. A Thermoneutrality. B Cold exposure. Squares: feathered skin temperature (T_{sk}); Circles: surface temperature (T_s); Triangles: ambient temperature (T_a). Numbers above and below points represent sample sizes. Half-filled circles represent values during moult in one penguin.

4.3 RESULTS

The metabolic response to wind in the little penguin differed considerably between thermoneutral and cold temperatures (Figure 4.2). At thermoneutrality metabolic rate did not differ with windspeed and remained relatively constant at an overall mean (±SD) of 3.75± 0.26 Watts (n=31).

During moderate cold exposure, however, metabolic rate (H) increased linearly with windspeed as:

$$H \text{ (Watts)} = 4.56 + 0.316\ V \qquad (4.1)$$

$$(r = 0.852,\ F_{1,24}=63.7,\ p < 0.001,\ s^2_{y.x}=0.114,\ s_b=0.040)$$

where V equals windspeed (m/s). If windspeed is expressed as the square root of air velocity ($V^{0.5}$) the relationship between metabolic rate and windspeed at low temperature becomes:

$$H \text{ (Watts)} = 4.21 + 0.786\ V^{0.5} \qquad (4.2)$$

$$(r = 0.834,\ F_{1,24}=54.63,\ p < 0.001,\ s^2_{y.x}=0.127,\ s_b=0.105)$$

Feathered skin and surface temperatures decreased with windspeed as shown in Figure 4.3. At thermoneutrality feathered skin temperature gradually declined by 2.8°C from 34.2°C at zero windspeed across the range of windspeeds tested. During cold exposure skin temperature decreased by 0.7°C from an initial value of 29.2°C at zero windspeed to 28.5°C at 0.8 m/s and remained relatively constant at higher windspeeds.

Surface temperature at thermoneutrality showed a gradual decline of 2.8°C with increasing windspeed from an initial value of 25.4°C at zero windspeed. The decrease in surface temperature with windspeed during cold exposure was 4.9°C from a zero windspeed value of 13.0°C. At the highest windspeed tested surface temperature was 1.1°C above ambient at thermoneutrality and 2.2°C above ambient during cold

exposure.

Mean wing temperature at thermoneutrality was 1.6 ± 1.8°C (n=14) above ambient and showed no change with windspeed indicating that the wing remained vasoconstricted. Body temperature remained stable with windspeed at an overall mean of 39.0 ± 0.5°C.

Metabolic parameters measured in one penguin early in moult when the coat structure was opening and the feathers on the wing had been replaced were higher than normal values. Metabolic rate during moult at thermoneutrality was 5.88 $W/kg^{0.73}$ at zero windspeed, 43% greater than the mean normal value expressed in weight independant values. In contrast to an unchanged rate of metabolism with windspeed in non-moulting penguins at thermoneutrality, metabolic rate at 1.7 m/s was 6.02 $W/kg^{0.73}$. During cold exposure, metabolic rate during moult at zero windspeed was 7.40 $W/kg^{0.73}$, 49% greater than non-moulting penguins. At 1.7 m/s metabolism during moult was 8.23 $W/kg^{0.73}$. Body temperature during moult experiments was 40.3 ± 0.6°C. Feathered skin and surface temperatures were also elevated above normal values as shown in Figure 4.3.

4.4 DISCUSSION

4.4.1 Metabolic rate

This study shows that the effect of wind upon metabolism varies with environmental temperature. Although increased windspeed results in a greater capacity for convective heat transfer to the environment (Gates 1980) little penguins maintained resting levels of metabolism at thermoneutrality at windspeeds up to 4.7 m/s. Outdoor experiments on king and emperor penguins similarly report that metabolic rates within thermoneutrality remain at resting levels at windspeeds up to 4.5-5.0 m/s (Barre 1980, Le Maho et al. 1976). This response in penguins contrasts with reports of increased metabolism with windspeed at moderate temperatures in quail, white-crowned sparrows, and long-eared owls (Goldstein 1983, Robinson, Campbell and King 1976, Wijnandts 1984).

The constant rate of metabolic heat production at thermoneutrality in this study implies little change in the total heat transfer coefficient estimated from the conventional formula for calculating whole body conductance (equation 2.5). Since wind increases convective heat loss, changes in partitional heat transfer may be observed by considering series conductances across the body, feathers, and boundary layer (section 4.4.3). Once a minimal level of conductance has been reached, increased windspeed will result in increased heat production. This result was observed in the little penguin below the lower critical temperature where wind was associated with an increase in metabolic rate. Wind may also be expressed in terms of a reduced effective temperature (Bakken 1980). Other avian studies which report increased heat production within thermoneutrality were close to the lower critical temperature of each species studied (Goldstein 1983, Robinson et al. 1976, Wijnandts 1984).

It is often reported that in common with equations for forced convective heat loss from geometrical shapes, convective heat loss in animals varies with the square root of windspeed (Bakken et al. 1981,

Evans and Moen 1975, Gessaman 1972, Hayes and Gessaman 1980, Kelty and Lustick 1977). The value of this exponent, however, varies considerably depending upon shape and flow characteristics between animals (Campbell, McArthur, and Monteith 1980, Goldstein 1983, Mitchell 1976). A linear increase in heat production with windspeed has been reported for quail (Goldstein 1983) and small mammals (Chappell 1980b). A linear decrease in coat insulation with windspeed may be common to many animals (Campbell et al. 1980). Cena and Clark (1979) suggest that other factors such as pressure gradients, which depend upon the square of wind speed, may also affect heat loss in relation to windspeed. Equations 4.1 and 4.2 in this study show that both windspeed (m/s) or the square root of windspeed ($m/s^{0.5}$) may be related to metabolic rate in cold exposed little penguins.

The metabolic response of the little penguin to wind may be compared with other birds from the equation of Goldstein (1983) which predicts the slope of the relationship between metabolism and the square root of windspeed as a function of body mass and temperature. From Goldstein (1983):

$$b = 0.0092m^{0.66}\Delta T^{0.32} \quad (4.3)$$

where m is body mass (grams) and ΔT is the temperature difference between ambient and the lower critical temperature. Little penguins in this study were approximately 5°C below their lower critical temperature (section 2.3.1) for which Goldstein's equation predicts a slope of 1.37 $W/(m/s)^{0.5}$ for a hypothetical 895 g bird. This value is 1.8 times that calculated for little penguins in this study (0.775 $W/(m/s)^{0.5}$, equation 4.2).

This study demonstrates that the relatively high heat transfer coefficients in penguins discussed in Chapter 2 impose no significant disadvantage during cold exposure. Minimal conductance values in penguins are derived from studies in metabolism chambers where air speeds are relatively low. Indeed, as shown above, the low metabolic

response to wind in the little penguin suggests that penguins in their natural environment may enjoy a substantial thermal advantage compared to other birds. As such, penguin plumage is very efficient in withstanding disorganization and penetration by wind due to its rigid structure of short, stiff, overlapping feathers (Le Maho et al. 1979, Stonehouse 1967).

4.4.2 Posture

Many birds orientate towards the prevailing wind direction presumably to avoid ruffling and penetration of the feather coat (Goldstein 1983, Lustick, Battersby, and Kelty 1978). By contrast, little penguins in this study maintained a standing posture with their backs to the wind at all windspeeds tested. This may be due to a preference by the penguin to look out of the windtunnel (which in itself indicates that the windspeeds used did not provide a considerable thermal drain). Alternatively, a penguin has a more upright stance than other birds and the angle of wind incidence together with the rigid feather structure implies that facing into the wind would not confer any great advantage. Indeed, as noted by Yeates (1971), pointing the head into the wind would expose the facial regions to greater heat loss. Adelie penguins exposed to a mean microclimate windspeed of 4 m/s varied in orientation according to the stage of their breeding cycle but most birds standing upright exposed their backs to the wind (Yeates 1971). Strong winds (8.5 m/s), however, resulted in incubating Adelie penguins facing into the wind (Spurr 1975a).

4.4.3 Partitional insulation

Insulation (I) is defined as the reciprocal of thermal conductance ($(m^2.°C)/W$). Since insulation is additive, estimates of changes in thermal resistance to heat transfer between the body and environment may be made by considering the partitional insulation provided by the body (I_b), plumage (I_p), and environment (I_e):

$$I_{tot} = I_b + I_p + I_e \quad (4.4)$$

During steady state conditions heat transfer across each

resistance is equal and directly proportional to the temperature gradient. Body, or internal insulation is given by:

$$I_b = (T_b - T_{sk}).\ SA_{skin}/(\dot{H} - \dot{E}_r). \quad (4.5)$$

where T_b is core temperature (°C), T_{sk} is the temperature of the skin beneath the feathers (°C), SA_{sk} is skin surface area (m^2), and $\dot{H} - \dot{E}_r$ is metabolic heat production minus respiratory evaporative water loss (Watts).

The external insulative layers (plumage and environment) are expressed as:

$$I_p = (T_{sk} - T_s).\ SA_{ext}/(\dot{H} - \dot{E}_r - \dot{E}_c) \quad (4.6)$$

$$I_e = (T_s - T_a).\ SA_{ext}/(\dot{H} - \dot{E}_r - \dot{E}_c) \quad (4.7)$$

where T_s is the surface temperature of the feathers (°C), T_a is ambient temperature (°C), SA_{ext} is external surface area (m^2), and $\dot{H} - \dot{E}_r - \dot{E}_c$ is metabolic heat production minus respiratory and cutaneous heat losses.

Skin surface area in this analysis was calculated assuming a Meeh value of 0.1 (Drent and Stonehouse 1971, Walsberg and King 1978a) whereas external surface area was calculated using a Meeh value of 0.087 previously determined for little penguins (section 2.2.3).

Evaporative heat loss was shown to be independant of windspeed in white-crowned sparrows (Robinson et al. 1976). Total evaporative heat loss was assumed to be 28% of metabolic rate at thermoneutrality and 9% of metabolic rate during cold exposure as determined for litle penguins by Baudinette, Gill, and O'Driscoll (unpublished manuscript). Birds have usually been regarded as having relatively

low rates of cutaneous water loss although this assumption does not appear to be applicable to all species (Dawson 1982). Comparing data from Marder and Ben-Asher (1983) and Marder (1983) gives cutaneous evaporative water loss as 50% of total evaporative water loss in the partridge (which has a limited ability to change cutaneous evaporation) and 70% of total evaporation in the pigeon at ambient temperatures of 20-25°C. Limited measurements of the contribution of cutaneous evaporation from other birds in the absence of heat stress cluster around 50% of total evaporative heat loss with the pigeon being rather high in comparison (Dawson 1982). Cutaneous evaporative water loss was therefore assumed to contribute 50% of total evaporation in the little penguin for calculations of dry heat fluxes.

The role of corneal evaporation and the rete opthalmicum in relation to convective cooling with increased windspeed in the little penguin is unknown. Although corneal evaporation and the rete may act as a cooling mechanism for the brain during heat stress in flight (Pinshow et al. 1982) the rete also reduces heat loss from the exposed eyes during cold conditions (Frost et al. 1975, Midtgard 1983).

Detailed analysis of heat transfer from animals is complex due to variation with different areas of the animal. Models provide accurate measurements of such regional heat loss but do not allow for physiological regulation. Although heat loss in the little penguin was measured on a whole body basis, the equations describing partitional insulation will vary in accuracy depending on variation between measurements of temperature gradients across the breast and mean values for the whole body.

Surface temperatures vary in birds with the head implicated as the region of greatest heat loss per unit surface area (Hill, Beaver, and Veghte 1980, Veghte and Herreid 1965, Despin, Le Maho, and Schmitt 1978). Little penguins in this study wore masks for measurement of metabolic rate which may have restricted heat loss although this was not quantified due to the target size of the non-contact thermometer used in experiments. Wing temperature of little penguins was also slightly cooler than the surface temperature of the contour feathers.

If surface temperature is weighted for these variations according to proportional surface area measured on frozen penguins the mean surface temperature is given as:

$$T_s = 0.1T_{(head)} + 0.70T_{(contour)} + 0.2T_{(wings + feet)} \quad (4.8)$$

Assuming that surface temperature of the head is approximately 3°C higher than surface temperature of the contour feathers as in the peruvian penguin (Despin et al. 1978), then mean surface temperature at thermoneutrality was 0.3°C less than measured at the contour feathers at zero windspeed and 0.4°C greater than contour surface temperature at 4.7 m/s. This variation is less than absolute differences in temperature of the different regions due to the divergence of head and peripheral temperatures. The error generated from use of contour feather surface temperature rather than a mean value is less than 10%.

Surface temperatures may also vary between windward and leeward sides during forced convection (Clark and Toy 1975, McArthur and Monteith 1980). Although convection coefficients vary around a cylinder in wind, the convection coefficient on the lee side is shown

TABLE4.1
PARTITIONAL INSULATION OF LITTLE PENGUINS WITH WIND AT THERMONEUTRALITY AND COLD EXPOSURE

	V	I_b	I_p	I_e	I_{tot}
	(m/s)		m^2 °C/W		
Thermoneutrality:					
Normal values	0.1	0.14	0.29	0.11	0.54
	0.8	0.16	0.27	0.09	0.52
	1.7	0.17	o.28	0.07	0.53
	3.3	0.19	o.29	0.05	0.53
	4.7	0.22	0.27	0.03	0.51
Moult	0.1	0.10	0.14	0.09	0.33
	1.7	0.10	0.18	0.06	0.34
Cold exposure:					
Normal values	0.1	0.21	0.32	0.13	0.66
	0.7	0.21	0.33	0.11	0.65
	1.7	0.21	0.33	0.08	0.62
	3.3	0.19	0.31	0.05	0.55
	4.7	0.17	0.30	0.03	0.50
Moult	0.1	0.10	0.24	0.12	0.46
	1.7	0.10	0.25	0.07	0.42

V is windspeed; I_b body insulation; I_p plumage insulation; I_e environment insulation; and I_{tot} total insulation. Normal insulation values were calculated from data in Figures 4.1 and 4.2

Insulation during moult derived from one penguin only.

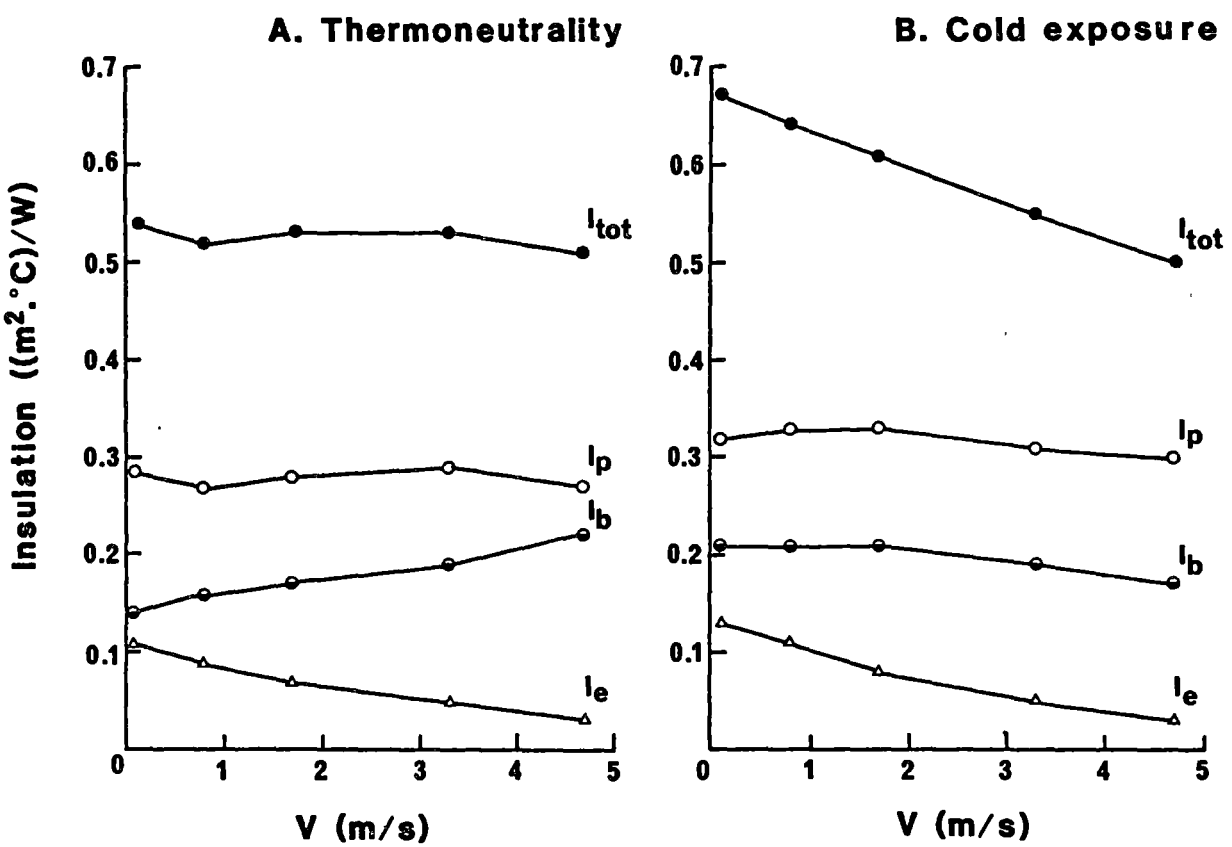

Figure 4.4 A,B. Partitional insulation in little penguins with windspeed calculated from equations in text. A Thermoneutrality. B Cold exposure. Closed circles: total insulation (I_{tot}); Open circles: plumage insulation (I_p); half-filled circles: body insulation (I_b); triangles: environmental insulation (I_e).

by Kerslake (1963) to be close to the mean coefficient for the whole cylinder. Due to the difficulty of obtaining radiant surface temperature at the windward side of penguins in the wind tunnel, surface temperature variations between windward and leeward sides of the penguin were assessed from measurements of 42SWG thermocouples glued to the surface of dorsal and ventral feathers. Such thermocouple measurements differed from those with the non-contact thermometer and gave a greater temperature gradient between surface and ambient temperature particularly at low windspeeds. The temperature difference between leeward and windward sides diminished with increasing windspeed; surface temperatures at the windward side were approximately 1.0°C lower than the leeward side at windspeeds less than 1.7 m/s. At higher windspeeds this difference was 0.5°C. Ventral surface temperatures were corrected by 0.5°C at windspeeds less than 1.7 m/s and 0.3°C at higher windspeeds.

Surface area as determined by the parafilm technique of Walsberg and King (1978a) may also substantially underestimate surface area in ptiloerected birds (Hill et al. 1980), although this error may be modified to an unknown extent by other thermoregulatory behaviours such as retraction of the head.

Changes in partitional insulation in the little penguin in response to increased windspeed at thermoneutrality and cold temperature are shown in Table 4.1 and Figure 4.4. Total insulation at zero wind speed during cold exposure (0.66 (m^2.°C)/W) was greater than zero windspeed at thermoneutrality due to increased body and feather insulation. This value was also larger than 0.55 (m^2.°C)/W given for dry insulation of little penguins below thermoneutrality calculated from internal and external conductances (section 2.4.7) although the difference was not significant ($t_{1,20}$ = 0.48, $p < 0.5$).

Body insulation at zero windspeed during cold exposure in little penguins (0.21 (m^2.°C)/W) is extremely high for birds (cf. Hill et al. 1980) and approaches the maximum values given for vasoconstricted tissue in large mammals (Mount 1979). This large resistance results in low feathered skin temperature. Skin temperatures in this study were similar to those given for the little penguin in section 2.3.1. Low skin temperatures appear to be common to other penguin species (Barre 1984, Drent and Stonehouse 1971, Kooyman et al. 1976, Le Maho

et al. 1976). However, Jarman (1973) reported that tissue insulation accounted for only 1.5% of total insulation in the emperor penguin in still air near its lower critical temperature with skin insulation contributing another 12.5% of total insulation.

What is the reason for high body insulation in the little penguin? No measurements of blubber thickness were made in this study. Subcutaneous fat does not appear to be necessary for the high body insulation as three penguins drowned in a fishing net and sent to me by Tasmanian National Parks and Wildlife Service had minimal amounts of subcutaneous fat. Le Maho et al. (1981) note (without detail) that overall body insulation in gentoo penguins does not change during fasting despite substantial changes in body fat. The thermal conductivity of human muscle and fat is approximately 0.39 and 0.20 W/(m.°C) (Hatfield and Pugh 1951). The observed value of body insulation can then be calculated to form the equivalent of a 4.3 cm layer of fat or 8.1 cm of vasoconstricted muscle. This simple analysis indicates that, taken as an average over the whole body and ignoring countercurrent heat exchange, the outer 2-4 cm forms a cooled peripheral shell. This corresponds well with the observed decrease in shallow cloacal temperature during cold exposure (section 2.3.1). The increase in body insulation with windspeed at thermoneutrality indicates that body resistance is actively controlled by changes in blood flow.

Plumage insulation in little penguins at zero windspeed during cold exposure (0.32 (m^2.°C)/W) was 10% higher than at thermoneutrality (0.29 (m^2.°C)/W) presumably due to enhanced ptiloerection. Comparisons of plumage insulation made for the little penguin in this study and those determined for other birds is difficult. Neild (1968, in Stonehouse 1970) gave the insulation of little penguin pelts as 0.23 (m^2.°C)/W although data also given for yellow-eyed penguin (0.30 (m^2.°C)/W) and emperor penguin pelts (0.33 (m^2.°C)/W) appear to be low compared to the insulation of Adelie and gentoo penguin pelts (0.52 and 0.57 (m^2.°C)/W) from Kooyman et al. (1976).

Evans and Moen (1975) reported plumage insulation of sharp-tailed grouse (of similar size to the little penguin) to be

0.49 (m^2.°C)/W whereas Wathes and Clark (1981) found the insulation of chicken pelts to be 0.37 (m^2.°C)/W. Cena and Clark (1979), however, note that insulation values of animal coats determined on flux plates may be reduced by a factor of two or more in vivo. Hill et al. (1980) calculated the plumage insulation of live 11 g chickadees to be 0.36 (m^2.°C)/W at 10°C and 0.43 (m^2.°C)/W at -16°C, values which exceed my estimation for the little penguin.

Although the plumage insulation in little penguins appears to be low compared to other birds, the thermal conductivity through the feather layer is not excessively high. Plumage thickness of little penguins was determined with a pair of calipers to be approximately 0.8 cm (Table 2.5) which combined with plumage insulation at thermoneutrality gives an estimated thermal conductivity of 28 mW/(m.°C). This is similar to the thermal conductivities calculated from the data for chickadees at 10°C (26 mW/(m.°C)), Adélie and gentoo penguin plumage (32 mW/(m.°C) and 46 mW/(m.°C)) and grouse plumage (30 mW/(m.°C)). By comparison the thermal conductivity of still air is 26 mW/(m.°C) at 20°C (Campbell et al. 1980).

Environmental resistances to heat transfer in the little penguin were equal at thermoneutral and cold temperatures. As expected from biophysical theory, environmental insulation decreased non-linearly with windspeed at both thermoneutral and cold temperatures. At thermoneutrality decreased environmental insulation with increasing windspeed was compensated by a 60% increase in body insulation so that total insulation remained relatively constant at 0.53 ± 0.01 (m^2.°C)/W. Body insulation at 4.7 m/s was similar to that observed at zero windspeed during cold exposure. No consistent changes in plumage insulation were noted.

These results show that during cold exposure the decrease in environmental insulation with wind resulted in a linear decrease in total insulation since body and plumage insulation could not be further enhanced. Although the decrease of 0.17 (m^2.°C)/W in total insulation was substantially due to the change in environmental resistance (0.09 (m^2 .°C)/W) there were also smaller decreases in both body (0.04 (m^2.°C)/W) and plumage (0.03 (m^2.°C)/W) insulation over the range of windspeeds tested.

Wind penetration within fur or feathers greatly increases convective heat loss (Hayes and Gessaman 1980, Kelty and Lustick 1977, Tregear 1965). The decrease in plumage insulation above windspeeds of 1.7 m/s in this study may be due to slight air penetration or increasing air pressure gradients resulting in enhanced convection within the feathers (Davis and Birkebak 1975, Cena and Clark 1980). This result was observed only during cold exposure where ptiloerection opens the coat structure. Unchanged plumage insulation at thermoneutrality indicates the overlapping feathers comprised a effective barrier to wind penetration. Another possible component of reduced coat insulation with wind, compaction of the fur or feathers (Gates 1980), appeared to be of minor importance to little penguins due to the rigid nature of the feather shaft.

Since the degradation of plumage insulation over the range of windspeeds tested during cold exposure was relatively small it is unlikely that the decrease in body insulation in these conditions was a direct result of cooling by wind. Further, as the extremities were excluded from this analysis, the change in body insulation was not the result of inhomogeneity of heat loss over different parts of the body as discussed by McArthur (1981). A possible explanation may be greater blood flow to muscles associated with increased shivering intensity with windspeed.

4.4.4 Moult

The increased metabolic rate observed during moult in one little penguin corresponds with previous reports that moult in penguins is associated with increased energy costs (Croxall 1982, Le Maho et al. 1976, Le Resche and Boyd 1969). Groscolas (1978) reported that moulting emperor penguins had an elevated body temperature approximately 1°C above normal levels. These additional energy costs are presumably due to the cost of feather synthesis and a decrease in insulation since moulting emperor penguins were observed to shiver at air temperatures 10°C above their normal lower critical temperature (Le Maho et al. 1976).

Values for partitional insulation during moult in a little penguin are given in Table 4.1. Insulation was calculated as for non-moulting penguins except that total evaporative heat loss was assumed to be 10% of metabolic heat production at thermoneutrality and 3.5% of metabolic rate during cold exposure (Baudinette, Gill, and O'Driscoll, unpubl. manuscript). Moult resulted in a reduction in both body and plumage insulation as compared to non-moulting penguins. Reduced body insulation was presumably related to high skin blood flow associated with growth of new feathers. New feather growth may have also resulted in lower plumage insulation although a substantial ptilomotor response during cold was observed. The increase in total insulation with cold exposure during moult (0.13 (m^2.°C)/W) was derived from increased plumage insulation and was similar to that seen in non-moulting penguins.

Increased windspeed (1.7 m/s) during moult as observed for non-moulting penguins, primarily resulted in reduced environmental insulation. At thermoneutrality total insulation remained constant due to an increase in plumage insulation rather than from changes in body insulation seen in non-moulting penguins. Body insulation during cold exposure and wind remained low, implying little capacity for altering vascular resistance.

These partial results indicate that moult confers a low plumage insulation and low body insulation with wind and during cold exposure. Penney (1967) noted that moulting Adelie penguins seek shelter from wind. However, insulation values in this study were derived early in moult when the new feathers are growing beneath the shaft of the old feather. Groscolas (1978) notes that by the time of moult per se in emperor penguins when old feathers are lost, new feather growth is completed so that insulation may approach normal levels.

4.5 SUMMARY

The metabolic response to wind in the little penguin varied with temperature. At thermoneutrality increased convective heat loss with wind was compensated by an increase in body insulation. During cold exposure body and plumage insulation had attained maximal values whereupon increased windspeed resulted in a linear increase in metabolic heat production. The primary effect of windspeed upon partitional insulation at neutral and cold temperatures was a decrease in the insulation provided by the thermal boundary layer.

The relatively shallow plumage depth of the little penguin confers a low coat insulation in comparison with other birds. Body insulation, however, may change considerably and attains a very high maximal value. Windspeeds up to 4.7 m/s have little effect upon the thermal insulation of the plumage. The dense waterproof plumage of the little penguin thus appears to confer a lower rate of heat loss with wind than would be expected on the basis of body weight and temperature from other avian studies.

Moult in one little penguin was associated with increased energy costs and a greater rate of heat loss during exposure to moderate wind. Decreased insulation during moult was due to lower values of plumage and body insulation associated with new feather growth.

CHAPTER 5.

THE NATURE OF SLEEP

All birds and mammals sleep. Despite its prevalance, our knowledge of the importance and physiological changes associated with sleep remain unclear. Sleep becomes potentially significant in the study of metabolism and thermoregulation as it is claimed to be an energy conserving mechanism (Walker and Berger 1980).

This chapter is intended to provide a basis for the understanding of sleep in the little penguin (Chapter 6). It discusses the electrophysiological and neural correlates of sleep, its patterns in phylogeny, and possible functions.

5.1 Electrophysiological characteristics of sleep

Sleep research rests on the electroencephalogram (EEG). The EEG is a record of the fluctuating electrical activity of the brain which conveniently shows pattern changes with the state of vigilance (Bures et al. 1976, Cooper 1971, Irwin 1975, Klemm 1969, Thompson 1967). Such records of spontaneous brain activity from the scalp of animals consist of small voltages of 20 to 100 microvolts with frequencies of 1 to 40 Hz. Voltages derived from electrodes in direct contact with the brain are higher since they are not attenuated by the skull and scalp (Klemm 1969).

It is generally considered that the mammalian EEG represents summated extracellular postsynaptic potentials in the cortex paced from the thalamus (Brazier 1977, Cooper 1971, Martin 1981). An analogy of the generation of the EEG is a myriad of circuit elements producing graded rather than all-or-none discharges and having a high degree of interraction. In such systems oscillations in voltage start as soon as a certain degree of interconnectivity is reached (Petsche et al. 1980).

The general correlations between the mammalian EEG and vigilance

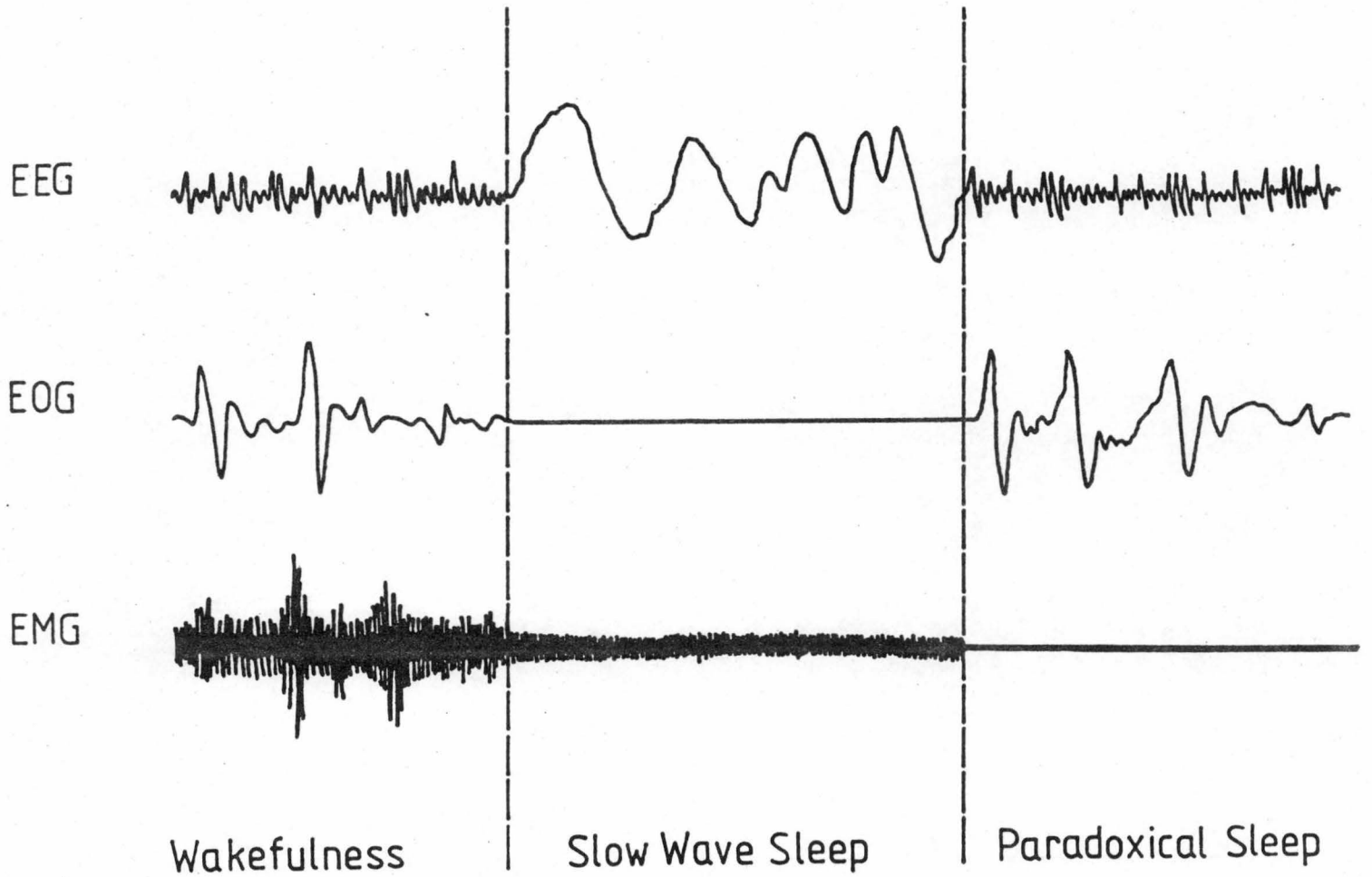

Figure 5.1. Electrophysiological correlates of sleep and wakefulness. See text for details.

are shown in Figure 5.1. Fast frequency low amplitude waves during alert wakefulness represent the neural activity obtained from millions of nerve cells involved in information processing. As the voltage changes are out of phase with each other, the result is a smear of random or desynchronized waves. During sleep slow frequency large amplitude (synchronized) waves appear. Such regularity implies that the cortex has been synchronized in its activity patterns. Sleep is not, however, a unitary process. Sleep states in animals are generally divided into slow wave sleep (SWS; alternatively quiet sleep or NREM sleep) and paradoxical sleep (PS; alternatively active sleep or rapid eye movement (REM) sleep). PS is so called since the EEG resembles that of the waking state. Two other parameters are normally used in conjunction with the EEG for determining the state of vigilance: eye movements as recorded by the electro-oculogram (EOG) and muscle activity and/or electromyogram (EMG). The EOG is active in wakefulness and PS whereas the EMG is prominent only during wakefulness.

5.2 The uncertain boundary of sleep

Much to the disappointment of sleep researchers, animals do not obey a simple on/off mechanism in that they are either asleep or awake. It is necessary to introduce the concept of vigilance or arousal, a simple definition of which would be the readiness or ability of an animal to respond to changes in its environment (Koella 1982). This arousal mechanism can be divided into at least three components: (a) EEG arousal; (b) behavioural arousal; and (c) autonomic arousal which reflects the level of activity in the autonomic nervous system (Mills 1981).

Most sleep studies employ EEG arousal to score vigilance. A simple approach is to consider a continuum of vigilance levels: that is deep sleep; light sleep; drowsiness; and relaxed wakefulness through to highly activated states of attention associated with increasing amounts of desynchronized EEG activity as behaviour moves towards greater arousal (Yingling 1980).

These stages are well recognized in man. During wakefulness there are several distinct EEG waveforms (as defined from frequency)

and four stages of SWS are measured (Gaillard 1980, Martin 1981). In addition, paradoxical sleep may be non-homogeneous as it can be divided into tonic and phasic subsets identified by the prescence or absence of rapid eye movements (Remmers 1981).

By contrast, vigilance levels in animal studies (apart from primates) have usually been considered discontinuous and confined to the simple patterns in Figure 5.1. More detailed investigation, has not surprisingly, revealed a diversity of EEG waveforms and degrees of vigilance. For example, Bouyer et al (1980) demonstrated several types of spontaneous rhythms from the anterior cortex of the cat during wakefulness. Quiet sleep in the cat can also be divided into SWS and spindle sleep (Jouvet 1967). Quiet sleep in the rat has also been shown by means of spectral analysis to consist of several types of SWS (Borbely and Neuhaus 1979). Discussion of the problems in distinguishing between quiescence, drowsiness and light sleep on the basis of EEG waveforms can be found in Chase (1972).

5.3 Neural mechanisms of sleep

Research into the neural substrates of sleep encompasses a broad field of literature unfortunately based on mammalian research. The summary that follows is not exhaustive or conclusive. Detailed information can be obtained from a number of extensive reviews (Jouvet 1967, Remmers 1981, Thompson 1967).

The reticular activating system (RAS) appears to have a predominant role in controlling sleep processes. The reticular formation comprises a number of neuronal pathways which extend from the brain stem to the thalamus and basal regions of the telencephalon. Siegal (1979) noted that it would be difficult for a sleep generating system to avoid using the widespread connections of the reticular formation to convey physiological changes throughout the brain.

Wakefulness is believed to be maintained by tonic excitation from the RAS which stimulates the lateral thalamic (LTh) nuclei. The

LTh functions as a relay nucleus whose cortical projections transmit excitatory signals to the cortex and maintain the desynchronized EEG characteristic of wakefulness. RAS stimulation also suppresses the medial thalamic nuclei (MTh). MTh cells inhibit LTh cells and thereby interrupt or gate the transmission of ascending impulses.

Onset and development of SWS involves (at least) three neuronal processes. Inhibition of the RAS from activation of basal forebrain areas and nucleus tractus solitarius results in the loss of facilitatory signals to the LTh and also releases the MTh from its previous suppression. Enhanced excitability of MTh cells generates powerful rhythmic excitatory and inhibitory postsynaptic potentials coincident with the development of slow waves and spindles in the cortex. Finally, cortical activity in pyramidal cells is depressed due to loss of ascending sensory input and activation of cortical inhibitory neurons.

The desynchronized EEG characteristic of PS and increased neuronal firing rates in the cortex suggest that the RAS and thalamo-cortical circuits are active. Input and output functions of the nervous system, however, are greatly impaired. During the tonic stage of PS motor neurons are inhibited, but during phasic stages powerful excitatory postsynaptic potentials at motor neurons may override descending inhibitory impulses often resulting in myoclonic muscular jerks. It appears that the stimulus driving PS originates from the brain stem region lying between the spinal cord and the pons.

In contrast to the concept of sleep onset as passively resulting from reticular deactivation, sleep can also be regarded as an active process induced by the raphe system. The raphe nuclei are a group of neural formations extending from medullary levels through the mesencephalon. Such cells secrete monoamines, such as serotonin. Since destruction of the raphe nuclei results in the loss of SWS, it was proposed that serotonin release induces SWS (Jouvet 1967). Webb and Dube (1981), however, note that disruption of the serotonergic system in rats produced negative results and discuss the evidence that other neurotransmitters (catecholamines, acetylcholine and polypeptides) are also implicated in various sleep processes.

Connections between the RAS and serotinergic systems remain enigmatic. Morrison (1979) noted that cats pharmacologically deprived of serotonin are eventually able to sleep inferring that other systems or neurochemical mechanisms can compensate for serotonin depletion.

5.4 Phylogeny of sleep

5.4.1 Mammals

The general electrophysiological correlates of SWS and PS appear in all eutherians and marsupials so far investigated. PS has not been shown in electrophysiological recordings of sleep in the echidna despite extensive effort (Allison et al. 1972). Griffiths (1978, p181), however, refers to an account in Bennett (1835) in which two captive juvenile platypus often appeared to dream of swimming when asleep: "Their forepaws in movement as if in the act". Further investigation of monotreme sleep may be directed towards young animals (as noted by Allison et al. 1972, Griffiths 1978). It is intriguing that Noback and Allison (1972) reported the neural structures thought to be involved in the generation of PS are present in the brainstem reticular nuclei of the echidna.

5.4.2 Birds

Recalling that EEG activity originates in the cortex it is perhaps surprising that the conventional signs of sleep are seen in birds. In contrast to the mammalian cortical mantle the avian forebrain is characterized by an unlaminated structure called the hyperstriatum. Some lamination is present in the dorsal portions of the forebrain (the Wulst, corticoid, and parahippocampal regions) (Benowitz 1980). Despite these morphological differences, the hyperstriatum and mammalian neocortex are often considered homologous (Van Tienhoven 1969). Cohen and Karten (1974) noted that each major cell group in the avian telencephalon recieves specific sensory projections in a manner remniscent of mammalian sensory cortex.

Northcutt (1981), however, has emphasized that neural pathways in different orders may not subserve the same function. Hence there is a need for caution in interpreting sleep in birds as being derived from the same mechanisms in mammals.

Amlaner and Ball (1983) define a wide range of behavioural sleep characteristics in birds such as pseudo-sleep, rest-sleep posture, and sleep posture. Such diversity indicates an uncertain boundary between behavioural sleep and wakefulness in birds. EEG records from awake quiescent birds often show slow waves (Berger and Walker 1972, Key and Marley 1962, Ookawa 1972, Rojas-Ramirez and Tauber 1970, Tradardi 1966, Zepelin et al. 1982). This problem could be related to debate on drowsiness and continuum of vigilance levels; Koella (1982) noted that vigilance levels vary between different neural systems wherein the bursts of slow EEG waves may reflect a decrease in reactivity of neural networks subserving "higher functions". Different EEG records during quiescence between mammals and birds may also result from the morphological differences in neural organization noted above. Lack of a laminated neocortical layer in birds infers discharge relays from the thalamus may not be suppressed by the spontaneous cortical activity seen in mammals.

5.4.3 Ectotherms

Since ectotherms do not show clearly differentiated EEG records, the status of sleep in the "lower" vertebrates is controversial. While sleep is a cerebral activity, which may be expected to show different functional patterns during sleep and wakefulness, an exclusive definition of sleep based on mammals and birds may be too simplistic.

There is no true cortex (ie. a homologous structure to mammalian neocortex) in amphibians and reptiles (Kappers et al. 1960). Broughton (1972) provided a phylogenetic survey of the neuroanatomical structures thought to be actively involved in the initiation of sleep states in mammals. EEG signals are only signs of sleep and not sleep itself as seen by pharmacological and lesion induced dissociation of EEG and behaviour (Bradley 1968, Granda and Maxwell 1978, Thompson 1967). Although human infants undoubtedly

sleep, they do not develop characteristic slow waves and spindles in EEG records until about one month of age (Lindsley and Wicke 1974). It is perhaps optimistic to expect less differentiated nervous systems to display the same signals that we expect from higher vertebrates.

i) Fish and amphibians

Kharmanova and Lazarev (1979) and Khomuteskaya et al. (1979) have reviewed Russian work on sleep-like states (SLS) in fish and amphibians. These SLS differ from wakefulness by typical postures, loss of alertness, and considerable bradycardia. Two forms of SLS are proposed for fish characterized by "plastic" and "rigid" muscle tones. Amphibians show an additional form of SLS accompanied by muscle relaxation, closed eyes, and evidence of small changes in the EEG (as revealed by power spectra of the EEG).

ii) Reptiles

Evidence for sleep in reptiles can be separated into sleep-related behaviour (as seen in fish and amphibians) and electrophysiological correlates of sleep.

Reptiles show signs of behavioural sleep (as contrasted to thermoregulatory behaviour) judged from the following criteria (Flanigan 1972):

a) assumption of a stereotypic or species-specific posture;
b) maintenance of behavioural quiescence;
c) elevation of behavioural threshold reflected in the intensity of arousal threshold and/or frequency or latency in arousal response;
d) state reversibility with stimulation.

These standards are argued to have been fulfilled in turtles (Flanigan 1974, Flanigan et al. 1974), lizard (Tauber et al. 1968) and the caiman (Flanigan et al. 1973, Meglasson and Huggins 1979). Not surprisingly, researchers who conclude reptiles do not sleep disdain any signs of behavioural sleep, relating behaviour to thermoregulation (Walker and Berger 1973) or describe a relatively

continuous state of inactivity (Van Twyver 1973).

Electroencephalograms of reptiles (reviewed by Belekhova 1979) display remarkable disparity. These signals are usually correlated with activity or rest and behavioural quiescence and can be divided into pattern analysis of EEG waveforms and spike and sharp wave activity. Small changes in EEG activity between alertness and behavioural quiescence (albeit contradictory) have been reported for caimans (Flanigan et al. 1973, Meglasson and Huggins 1978, Rechstaffen et al. 1968, Warner and Huggins 1978), turtles (Flanigan 1974, Flanigan et al. 1974), and a lizard (Huntley et al. 1978). By contrast, several researchers report no correlation between EEG and behaviour (Susic 1972, Van Twyver 1973, Walker and Berger 1973).

Part of the variability in the reptilian EEG may be ascribed to temperature (Belekhova 1979, Huntley and Cohen 1980, Meglasson and Huggins 1979) since the amplitude and frequency of the EEG diminishes with decreasing temperature until isoelectric records are obtained (Parsons and Huggins 1965, Van Twyver 1973, Walker and Berger 1973). In addition to a sub-optimal signal in studies at sub-optimal temperatures, sleep behaviour may be diminished.

A characteristic feature of the reptilian EEG are large amplitude spikes derived from most areas of the telencephalon. Spike activity is claimed to increase with behavioural sleep or quiescence (Flanigan 1973, Flanigan et al. 1973, Tauber et al. 1966, Walker and Berger 1973). The reptilian spike is suggested to be analogous to the limbic system spike in mammalian slow wave sleep (Hartse and Rechstchaffen 1982, Hartse et al. 1979).

However, in contradiction to the concept of spikes as an expression of a primitive sleep system, Huntley and Cohen (1980) found that sharp wave activity decreased with behavioural sleep. Moreover, Meglasson and Huggins (1979) and Tauber et al. (1968) claim no relationship between spike rate and behavioural state.

The relative absence of the mammalian patterns of sleep could be interpreted that sleep states are not fully developed in reptiles. This was the conclusion of Kharmanova and Lazarev (1979) who

classified reptiles as having "intermediate sleep". Alternatively the conflicting evidence suggests sleep may be polyphyletic in reptiles.

5.5 Sleep patterns

Sleep is a cyclic phenomenum associated with other circadian rhythms. Sleep is also subject to ultradian rhythms, a well known example being the periodic occurrence of PS every 90 minutes in human sleep. Kleitman (1963) suggested that periodic recurrence of PS episodes was part of a general rhythm of the central nervous system called the basic rest-activity cycle. This concept proposes an ultradian rhythm present across time but more obvious during sleep. Correlates for a rest-activity cycle in wakefulness, however, have proved elusive (Webb and Dube 1981). Also, like many theories of sleep, the rest-activity cycle hypothesis is derived from mammalian research. If we accept that PS epochs reflect this proposed rhythm, then birds would have a rest-activity cycle of approximately one minute as short PS periods are so interspersed throughout avian sleep.

Several authors have presented reviews which attempt to correlate the temporal characteristics of sleep and various parameters. Zepelin and Rechtschaffen (1974) gave correlations based on data from 53 mammalian species between sleep variables (total sleep time (TST), length of SWS and PS epochs, and cycle length) and metabolic rate, brain weight, gestation period, and life span. All sleep parameters except the percentage of PS were significantly correlated with the other variables. Zepelin and Rechtschaffen selected metabolic rate as the primary variable with the greatest influence on daily sleep time. This conclusion is surprising since in no instance did metabolic rate give the greatest correlation when compared to the other variables against any sleep parameter. In addition, each of the constitutional variables listed above are likely to be interdependant with each other, particularly with size or body mass (Calder 1981).

Allison and Cicchetti (1976) pursued the correlates of sleep further and presented evidence to suggest that body weight and overall danger (the susceptibility of predation when asleep)

accounted for 58 percent of the variability in SWS time in 39 mammal species. The best predictor of PS was found to be overall danger. Allison and Cicchetti, however, noted that only about 60 percent of the variability in SWS and PS could be accounted for by size, danger, and Zepelin and Rechtschaffens variables; and indicated the need for additional relevant variables. Of more importance they warned that such causal relationships can only suggest biological influences which relate to sleep.

Amlaner and Ball (1983) provide a similar analysis of sleep characteristics in wild birds based on behavioural observations. The amount of sleep, as in mammals, correlated with danger and exposure. Sleep time was also related to the amount of daylight and degree of communality during sleep. These variables still accounted for only 62% of the overall variance in total sleep time.

Accurate assessment of sleep parameters obtained from electrophysiological recordings may be better predictors than behavioural observation. Scherschlicht et al. (1981), however, point out that animals maintained in controlled conditions have a monotonous life with free access to food and water and are free to sleep whenever they feel inclined to do so. Such studies are not likely to show the normal sleep patterns of animals in the natural environment.

5.6 Functions of sleep

Why is it necessary to sleep? Certainly sleep is ubiquitous in mammals and birds and represents a rhythmic suspension of conciousness mediated by complex neurophysiological processes. As such it could be inferred that sleep is somehow essential to an animal's wellbeing. Although there are no lack of proposed answers to the possible functions of sleep, Rechtschaffen (1979) points out that there are serious methodological difficulties in testing any theory of sleep. Webb (1979) has discussed the prevalent hypotheses for supposed functions of sleep, each of which is briefly presented below.

5.6.1 Restoration

This is the most widely held intuitive notion about sleep. We feel tired before going to sleep and rested after sleep. Hence sleep is proposed as a period of recovery or restoration of physiological/neurological/psychological states. However the range of variables to supposedly be restored indicates little consensus.

Hartmann (1973) and Oswald (1974) consider SWS restores general bodily functioning whereas PS restores cerebral functions. Adam (1980) summarizes this position in terms of protein synthesis.

If sleep is a restoring process, then increased activity during wakefulness should result in increased sleep. However under freerunning conditions (no time cues), this proposed relationship was actually reversed- more activity is associated with less rest in man and chaffinches (Aschoff 1981)

On the other hand, Moruzzi (1966) proposed that paradoxical sleep restores only those neurons or synapses associated with concious behaviour, specifically learning and memory. Some indirect support for a memory-linked function of sleep is derived from research which demonstrates an increase in the amount of PS after learning has occurred. PS in domestic chickens increased in comparison with a control group after imprinting (Solodkin et al. 1980). Crick and Mitchison (1983) argue that PS may function as a reverse learning process by clearing undesirable patterns in cortical networks. This interpretation of sleep has some implications in sleep phylogeny. Ectotherms, with relatively stereotyped patterns of behaviour may be expected to need little sleep.

5.6.2 Ethology and instinct

As noted in section 5.5 animals regulate their sleep patterns in response to their lifestyle and environment. Sleep is sometimes considered an adaptive behaviour which imposes a period of inactivity during unfavourable periods of the animals niche (Meddis 1975, 1979).

An immediate difficulty with this interpretation is the presence of at least two sleep states.

5.6.3 Energy Conservation

Sleep (in particular SWS) functions to conserve energy (Allison and Van Twyver 1970, Berger 1975, Snyder 1966, Walker and Berger 1980). This position was summarized by Berger (1975): "...sleep constitutes a period of dormancy in which energy is conserved to partially alleviate the increased energy demands of homeothermy". Although metabolic and thermoregulatory correlates of the sleep/wake cycle are discussed in section (5.7) on the physiology of sleep there are a number of indirect correlates which have been advanced to support this hypothesis.

i) Sleep evolved coincidently with endothermy. Consequently, slow wave sleep (as such) is found only in mammals and birds (Allison and Van Twyver 1970, Berger 1975, Walker and Berger 1980). As noted in the section (5.5.3) the status of sleep in ectotherms is contentious. If sleep were shown to be the exclusive property of mammals and birds, then this gives only circumstantial evidence to energy conservation in sleep. However, if sleep in reptiles were shown to be analogous to mammalian and avian SWS, then the energy conservation hypothesis would be severely embarrassed.

ii) There is a close correlation between the development of SWS and homeothermy. SWS develops at that point when it would appear most profitable to conserve energy (Berger 1975, Walker and Berger 1980). An alternative explanation is that this correlation simply reflects the maturing nervous system, particularly when the hypothalamus (thermoregulatory control) also appears to be an important centre in the timing of a number of rhythms (Webb and Dube 1981).

5.7 Physiology of sleep

There have been a number of recent reviews on thermoregulation during sleep in mammals (Heller and Glotzbach 1977, 1980, Parmeggiani 1977, 1980). Central to these discussions are that sleep stages (SWS and PS) constitute altered physiological states. The thermoregulatory consequences of SWS and PS, however, differ greatly. SWS is believed to represent a lower set-point in body temperature regulation whereas PS is associated with a loss of temperature regulation.

5.7.1 Changes in brain and body temperatures during sleep

Since both sleep and body temperature are circadian rhythms, it is necessary to investigate their relationship with each other. The circadian rhythm of body temperature is not caused by the alternation of sleep and wakefulness (activity and rest); sleep does influence the level of decrease in Tb during the resting phase, whereas activity influences the level of increase during the day (Aschoff and Wever 1981). When human subjects are placed under free-running conditions (removal of all external time cues) the rhythm of Tb may be disassociated from the sleep/wake cycle so that Tb declines during wakefulness and increases during sleep. Hence temperature and sleep are believed to be driven by different circadian oscillators (Aschoff and Wever 1981).

Many workers have reported that brain temperatures decrease during SWS in a wide variety of mammals (cf Heller and Glotzbach 1977 for references). Sleep onset also appears to be associated with increased sensible heat loss (Haywood and Baker 1969, Roussel and Bittel 1979). This could be the passive result of decreased activity of sympathetic vasoconstrictor fibres during sleep (Mancia and Zanchetti 1980) although Geschickter et al. (1968) demonstrate that in man sweating increases with sleep onset. A decrease in brain temperature and increased heat loss may be regarded as an active adjustment towards a lower set point for body temperature regulation.

Examination of literature which report both brain and deep body

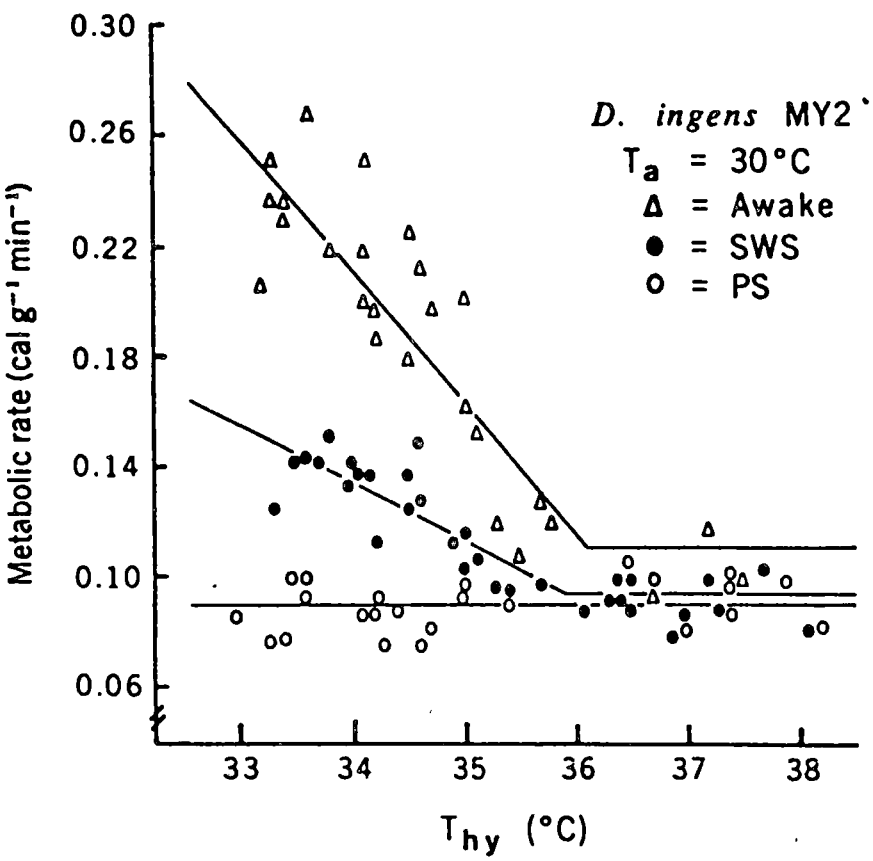

Figure 5.2. Relationship between metabolic rate and hypothalamic temperature wakefulness, slow wave sleep, and paradoxical sleep in a kangaroo rat. Slow wave sleep results in a decreased proportionality constant or slope of metabolic rate against hypothalamic temperature, and a small change in body temperature setpoint. During paradoxical sleep there is no change in metabolic rate with variations in hypothalamic temperature. From Glotzbach and Heller (1976).

temperatures, however, shows no clear change in T_b during SWS in the cat (Adams 1963, Delgardo and Hanai 1966), dog (Hayward and Baker 1969), and sheep (Hayward and Baker 1969). Mills et al (1978) showed that deep body temperature in man decreased with sleep onset regardless of circadian rhythm but that such changes were small compared to circadian variation. A potential decrease in core temperature with sleep may be related to an animal's thermal inertia, the length of sleep periods, and the ambient temperature.

In contrast to the reported decrease in temperature during SWS, brain temperature often increases upon the transition from SWS to PS (Heller and Glotzbach 1977). This increase may be related to concomitant measurements of peripheral vasoconstriction in the ears and nasal mucosa (Haywood and Baker 1969), although peripheral vasomotor activity appears to differ between species and is influenced by ambient temperature. Reports of peripheral vasoconstriction during paradoxical sleep are puzzling in view of general vasodilatation (Mancia and Zanchetti 1980) and a decrease in autonomic nervous activity in this sleep stage (Parmeggiani 1980). Changes in brain temperature may also be related to local tissue metabolic rates, changes in blood flow, or respiratory patterns (Heller and Glotzbach 1977).

5.7.2 Thermoregulatory processes during sleep

Detailed investigation of changes in control of body temperature during sleep was initiated by Glotzbach and Heller (1976) who investigated the relationship between hypothalmic temperature, metabolic heat production, and vigilance in kangaroo rats (Figure 5.2). During wakefulness and SWS in kangaroo rats there is a threshold hypothalamic temperature (T_{hy}) below which metabolic rate increased. The hypothalamic set point during SWS is below wakefulness and the rate of increase in metabolic rate in SWS was approximately half that found in wakefulness. Metabolic rate during PS is independant of T_{hy} and remains at basal levels. A decrease in thermosensitivity of the spinal cord of pigeons has also been observed during sleep (Graf et al. 1981).

These sleep-related changes in neuronal thermosensitivity are

usually related to a simple model of thermoregulatory control (Hammel et al. 1963):

$$R - Ro = k\ (T_{hy} - T_{set}) \qquad (5.1)$$

where Tset is the threshold hypothalmic temperature for metabolic heat production, k is a proportionality constant (W/°C), R is metabolic rate (Watts), and R_o is metabolic rate when $T_{hy} = T_{set}$ (taken to be basal). Heller (1978) notes that hypothalamic thermosensitivity (k) is inversly related to body size. Unless other parameters in equation 4.1 change in the opposite direction, this infers that the difference between metabolic rate in sleep and wakefulness at a constant difference between T_{hy} and T_{set} may diminish with size.

Heller and Glotzbach (1977) suggested that the downward resetting of hypothalmic sensitivity in SWS supported a lower level of body temperature regulation whereas during PS there is no regulation of body temperature. A change in body temperature set-point with SWS has also been shown in birds. In pigeons panting was enhanced during sleep at high temperatures and shivering suppressed at low temperatures in comparison to values during wakefulness (Graf et al. 1981). However, Hohtola et al. (1980) demonstrated that decreased shivering activity during sleep in the pigeon was also associated with enhanced ptiloerection.

During PS autonomic thermoregulatory effectors are severely reduced. Shivering and panting are curtailed during PS in mammals and birds (Parmeggiani and Rabini 1970, Graf et al. 1981) and PS in man is associated with low rates of cutaneous evaporation (Henane et al. 1977, Shapiro et al. 1974). Nicol and Maskrey (1980), however, demonstrated that panting in the Tasmanian devil is reduced but not abolished during PS. Libert et al. (1982, in Muzet et al. 1984) showed that when ambient temperature is increased during a bout of PS in man, local sweating rates increase. Hence thermoregulatory responses, albeit diminished, may persist during PS.

5.7.3 Metabolic rate during sleep

Most reports on metabolic rate during sleep are derived from experiments on man. Measurements of metabolism during sleep at night strongly reflect circadian influence (Webb and Hiestand 1975). Contiguous measurements indicate that metabolic rate correlates with the stage of SWS (Brebbia and Altschuler 1965, Haskell et al. 1981, Shapiro et al. 1984), although metabolic rate is higher during PS. Such differences are small. Haskell et al. (1981) reported a decrease of 4% between combined data for stage 2 and stages 3 and 4 SWS and a 4% increase between combined data for all SWS stages and PS.

The hypothesis that sleep influences metabolism in man is widely accepted (Benedict 1938). Unfortunately, few studies in man have compared heat production in quiet wakefulness with that in sleep, partly due to the predominance of the circadian rhythm (Brebbia and Altschuler 1965, Haskell et al. 1981, Shapiro et al. 1984, Webb and Hiestand 1975). Shapiro et al. (1984) report that mean heat production over the whole night (including circadian effect) is 9% lower than quiet wakefulness whereas heat production in stage 4 SWS is 14% lower than quiet wakefulness. This difference corresponds with earlier suggestions of a 7-10% suppression of metabolic rate during sleep in man (Benedict 1938, Passmore and Durnin 1955).

Roussel and Bittel (1979) reported that oxygen consumption in rats increased during wakefulness and decreased and plateaued during SWS. PS was associated with a further decrease in oxygen consumption. As rats are usually active when awake, these differences were predominantly ascribed to muscular activity. Toutain et al. (1977) found that metabolic rate decreased by 10% between sheep lying awake and during SWS with a further decrease during PS. A decrease in metabolic rate associated with PS was observed by Nicol and Maskrey (1980) in the Tasmanian devil particularly at low temperatures, as the difference between metabolism during SWS and that in PS increased.

Decreased metabolic rate with behavioural observations of sleep in birds have also been reported at thermoneutrality in the domestic fowl (Hutchinson 1954) and at low temperature in the black vulture

(Larochelle et al. 1982) and anhinga (Mahoney 1981).

A decrease in metabolic heat production during sleep in mammals and birds evokes problems in interpretation and comparison of resting metabolic rates (Benedict 1938). This is implicit in the definition of standard or basal metabolic rates which is obtained from awake animals (Bligh and Johnson 1973). Bartholomew (1977) notes that the term basal is unfortunate as it implies an absolute minimum. Although resting metabolism within the thermoneutral zone may be regarded as an obligate level of heat production associated with body functions necessary to sustain life, this level is in excess of that required to maintain body temperature (Dawson 1972).

It may be argued that an animal is not in steady-state conditions during sleep if sleep periods are relatively short. Roussel and Bittel (1979) and Toutain and Webster (1975) measured heat loss and heat production in relation to sleep in rats and ruminants. Sleeping animals in both studies lost more heat than was produced. The long sleep periods of man, as noted above, are associated with different levels of metabolism within sleep. Sleep could be then regarded as a transient rather than equilibrium state.

However, the conditions for measuring standard metabolism also favour sleep. The relatively low airflow rates normally used in such studies confer long time constants for gas exchange within the metabolic chamber. Hence, without continuous observation, periods of sleep are likely to be interspersed in metabolic records from quiet, undisturbed animals (particularly during the rest phase of the circadian rhythm).

A decreased metabolic rate during SWS is claimed to support the energy conservation theory of sleep (section 5.6.2). Torpor and hibernation in small mammals and the ringed turtle dove further appear to be an extension of SWS (Heller and Glotzbach 1977, Heller et al. 1978, Walker et al. 1981, Walker et al. 1983). Torpidity is therefore argued to represent an extension of the energy conserving properties of sleep. Although various degrees of controlled hypothermia have been recorded from several orders of birds, such departures from normal temperature regulation may be considered a

specific adaptation to extending limited energy reserves rather than a general trait available to all birds (Calder and King 1974, Dawson and Hudson 1970).

By contrast to an energy conserving role for SWS, the profound drop in metabolism to basal levels in PS is argued to provide greater opportunities for energy savings (Horne 1977, Nicol and Maskrey 1980). The energetic significance of sleep as a mechanism to conserve energy is examined in Chapter 6.

CHAPTER 6.

METABOLIC HEAT PRODUCTION AND SLEEP

6.1 INTRODUCTION

As reviewed in Chapter 5, thermoregulatory mechanisms vary as a function of sleep and wakefulness in mammals. Slow wave sleep (SWS) is accompanied by a regulated decrease in the set-point for body temperature regulation and paradoxical sleep (PS) is further associated with a profound inhibition of thermoregulatory responses (Heller and Glotzbach 1977, Parmeggiani 1980). In association with these changes in thermoregulatory functions, ambient temperature influences sleep. Total sleep time (TST) is maximal at thermoneutrality and the amount of sleep, particularly PS, decreases in hot or cold conditions (Parmeggiani and Rabini 1970, Sakaguchi et al. 1979).

Information on sleep in birds is relatively sparse compared to that for mammals. The electrophysiological indices of sleep in birds are broadly similar to those in mammals although PS epochs in birds are extremely brief (approximately 10s) (Goodman 1974, Ookawa 1972). Physiological changes during sleep in birds also appear to be similar to the mammalian pattern. Pigeons show a decrease in body temperature set-point during SWS and a cessation of shivering and panting was observed during PS (Graf et al. 1981). Hohtola et al. (1980) demonstrated that although shivering diminished during sleep at low temperatures in the pigeon, not all thermoregulatory responses were attenuated since ptiloerection during sleep was greater than that observed during wakefulness.

The decrease in thermoregulatory effector mechanisms during sleep has been regarded as support for the view that sleep is an energy conserving process (Walker and Berger 1980). Direct evidence for this proposal is scarce. There have been relatively few studies which have investigated sleep and metabolism in animals without

manipulation of hypothalmic or spinal cord temperature so that the importance of the observed thermoregulatory changes is unclear.

This study investigates the effect of sleep on metabolic energy expenditure in the little penguin at thermoneutrality and low ambient temperature. In addition, since body temperature regulation in birds follows a circadian rhythm which is actively adjusted between day and night (Graf 1980a,b), the influence of sleep upon this cycle was examined.

6.2 MATERIALS AND METHODS

6.2.1 Electrophysiological recordings

Electrodes were implanted under halothane anaesthesia for the chronic recording of electrophysiological correlates of sleep and wakefulness. EEG (electroencephalogram) electrodes were made from stainless steel or gold plated brass wood screws lying above the Wulst, parahippocampus, and hyperstriatum to record bipolar electrical activity of the brain. EOG (electro-oculogram) electrodes monitered eye movements. These electrodes consisted of fine copper or stainless steel wires with a gilded ball of solder at the end. These were inserted under the inner and outer canthus of one eye or under the outer canthus of both eyes. EMG (electromyogram) electrodes were used to record dorsal neck muscle activity in two penguins. The electrodes were made from fine multi-strand insulated stainless steel wires joined at the end by a ball of dental cement. A small area of teflon insulation was removed from each wire near the junction.

Lead wires from recording sites were soldered to a multipin socket which was then mounted on the skull with dental acrylic cement. These headpieces remained in place for two months and were removed from each bird when they became loose, presumably due to bone absorption around the screws. At least one week was allowed following surgery before experiments began.

Electrophysiological parameters were recorded on a Grass model 79D polygraph via a braided cable and slip ring connector. A strain gauge attached to the cable allowed detection of gross body movements. Chart speed was 5 mm/sec. Polygraph records were scored in 5 second epochs for sleep/wake states and each minute for metabolic analysis. Data from two penguins were also also recorded on magnetic tape for subsequent analysis of EEG characteristics.

6.2.2 Metabolic rate

Oxygen consumption and carbon dioxide production were simultaneously measured with a fast response open-circuit system to avoid mixing of air samples from different states of conciousness. A seven litre container immersed in brine served as the metabolic chamber. Temperature within the chamber was controlled by circulating brine through a heater/cooler unit. Room air was drawn through the chamber with a Thomas compressor and airflow rate (7.925 $\pm$ 1.445 l/min) was measured with a calibrated Gilmont flowmeter.

The outlet air was dried with silica gel and passed to the sample channel of a Servomex OA 184 oxygen analyzer. Atmospheric air simultaneously passed through a flowmeter and silica gel to the reference channel of the analyzer. Outputs from the sample and reference channels were compared by a Servomex RB-228 ratio box and recorded on a Rikadenki recorder with full scale deflection from 20 to 21% oxygen. Dry outlet air was simultaneously drawn through a Beckman LB-2 Medical Gas Analyzer for measuring carbon dioxide production, the output of which was also recorded as a 1% full scale deflection on the Rikadenki recorder.

The expected time lag for a steplike change in VO2 or VCO2 was calculated from the equation of Christensen (1947 in Westerterp 1977):

$$q/p = 1 - e^{(-F.t/V)} \quad (6.1)$$

where q/p = ratio of change in amount of O_2 or CO_2 carried off to change in oxygen consumption or carbon dioxide production (litres/min), F equals air flow rate (litres/min), V equals net volume (litres), and t equals time after start of change (min).

The volume of the chamber and airlines in the system was 9.23 litres and the volume of a little penguin was approximately 0.87 litres (section 2.4.8). Hence a 92% response could be expected in three minutes and a 97% response in four minutes after a stepwise change in expired gases in the system. From these estimated

equilibration times the first three minutes after a change in state of vigilance were ignored to account for the time lag in the system. The same time lag was used after gross body movements (as revealed by strain gauge fluctuations) to avoid the effects of activity.

Metabolic records were scored for sleep or wakefulness from polygraph recordings and the mean concentration of expired gases in sample periods determined by tracing the record onto standard weight paper which was weighed to the nearest 0.1 mg. Metabolic records were considered acceptable for analysis if (excluding lag time) they showed five minutes or more of continuous sleep or quiet wakefulness. Due to the very short period of PS epochs it was not possible to distinguish PS from SWS in metabolic analysis and hence both states have been considered as a single sleep state. Wing temperature was measured with a 36 swg thermocouple taped to the inside of the wing at the distal end of the humerus. Mean body weight of the six penguins used in sleep experiments was 0.96 $\pm$ 0.11kg.

6.2.3 Experimental procedure

Sleep-waking patterns and metabolic rates were measured at thermoneutrality (21.3 $\pm$ 2.71°C) and in cold conditions (-1.81 $\pm$ 2.17°C). No experiments were attempted above the upper critical temperature since little penguins cannot withstand prolonged exposure to heat stress (as shown in section 2.3.1 and discussed in section 3.3). During day experiments an equilibration time of one hour at thermoneutrality and two hours in the cold was allowed before data were collected. Measurements from day experiments were collected from 12:00 to 16:00h. For night experiments fasted penguins were introduced to the chamber at 17:00 h and data collected for a four hour period at least two hours after dusk. Illumination in night experiments was provided by a dim red light above the recording instruments.

Data for sleep and wakefulness represent mean data from each experiment. Sleep characteristics and sleep patterns from each experimental condition were compared by two-way analyses of variance with unequal but proportional subclasses. Metabolic data for sleep and wakefulness was compared with paired t-tests.

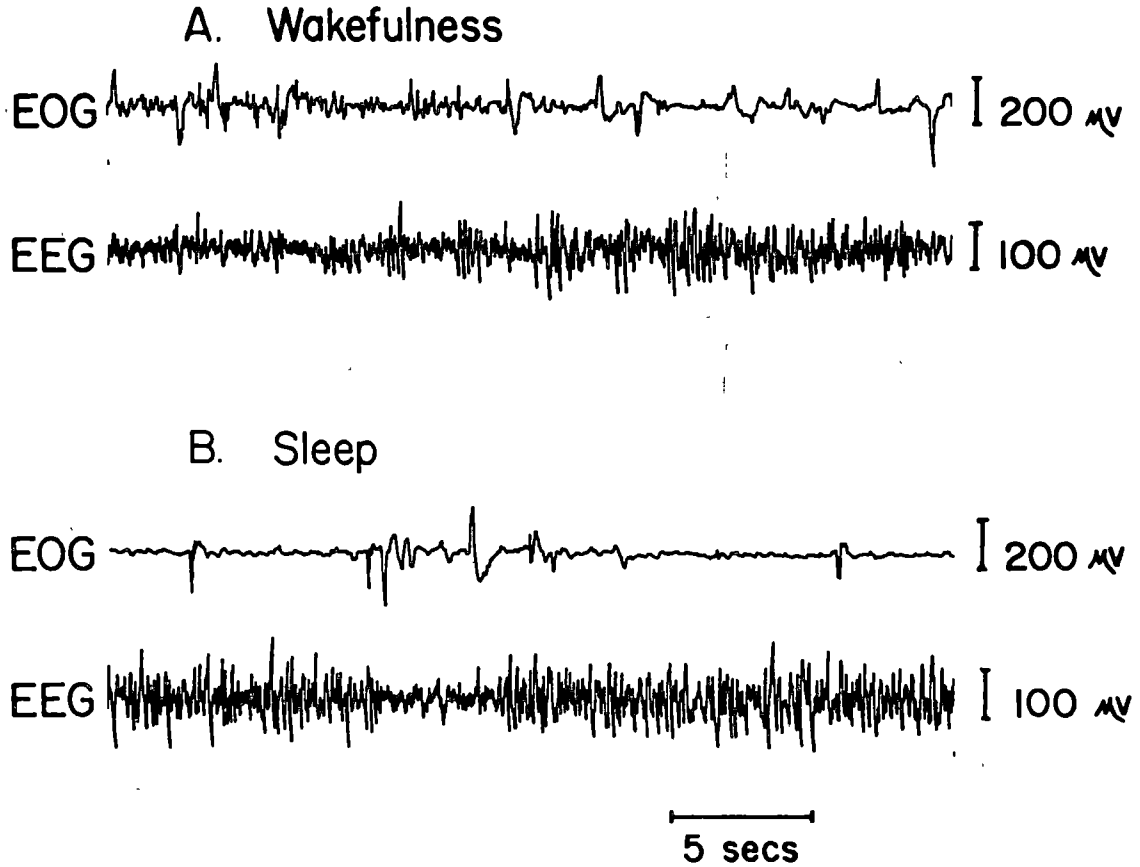

Figure 6.1 A,B. Polygraphic indices of sleep and wakefulness in the little penguin. A Wakefulness. B Slow wave sleep interrupted by an episode of paradoxical sleep. (EOG electro-oculogram measuring eye muscle activity; EEG electroencephalogram measuring surface electrical activity of the brain).

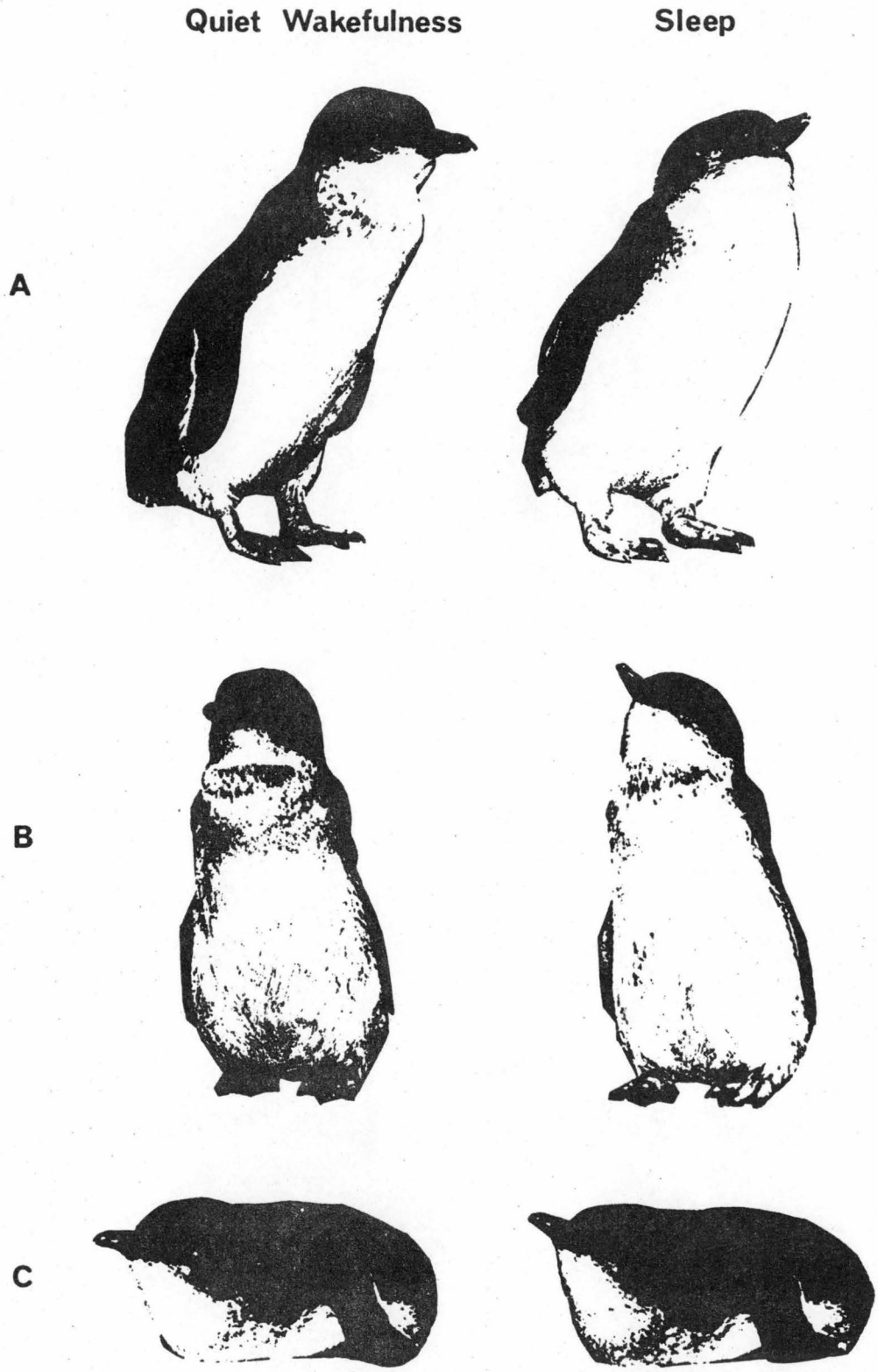

Figure 6.2 A,B,C. Sleep postures in the little penguin in comparison to quiet wakefulness. A: standing. B: resting on heels. C: lying down. In each posture sleep resulted in the head retracted into the body with the beak pointing slightly upwards.

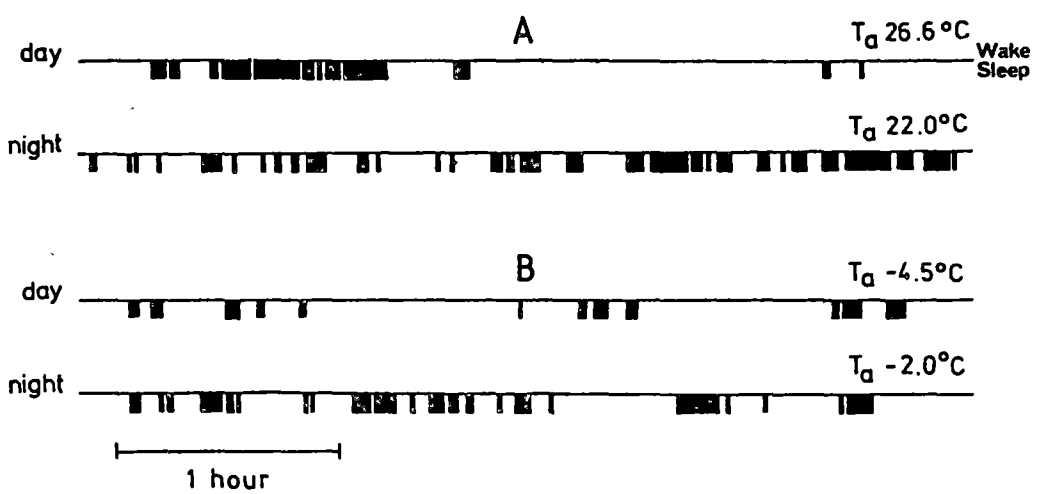

Figure 6.3 A,B. Sleep-waking patterns of a little penguin during four hour polygraphic recordings. Each minute was scored as either wakefulness or sleep (slow wave sleep plus paradoxical sleep) A Thermoneutrality. B Cold exposure. Areas shaded black represent periods of sleep.

6.3 RESULTS

6.3.1 Polygraph recordings and posture

Polygraphic indices of wakefulness and sleep in the little penguin are shown in Figure 6.1. Wakefulness was characterized by frequent eye movements and low voltage relatively high frequency EEG activity (50 μV, 13-17 Hz) interspersed with bursts of slow wave activity (130-180 μV, 8-11 Hz) of 1-2 seconds duration. Slow wave activity was more prominent during quiet wakefulness.

Penguins in their enclosure were observed to sleep either standing or lying down with the head retracted into the body and their beak pointing slightly upwards (Figure 6.2). Due to the small size of the chamber penguins slept upright in experiments. Polygraph records of slow wave sleep (SWS) (Figure 6.1B) showed no eye movements apart from small voltage fluctuations periodically interspersed throughout the sleep period. The EEG was characterized by synchronous activity of high voltage, relatively slow waves (100-240 μV, 8-12 Hz). Paradoxical sleep (PS) epochs of short duration were interspersed throughout SWS. These bouts were identified by clustered eye movements and desynchronized EEG patterns which resembled that seen in active wakefulness (<50μV, 13-14 Hz).

Neck muscle activity in little penguins correlated poorly with sleep and wakefulness. Although EMG bursts were associated with active wakefulness, the EMG was isotonic during quiet wakefulness and SWS. PS periods occasionally contained a transitory decrease in muscle tone but more often EMG bursts due to jerks of the head were observed.

6.3.2 Sleep-Waking Patterns

The amount of sleep observed in the little penguin varied as a function of its circadian rhythm and temperature. Figure 6.3 shows the temporal sequence and amount of sleep in the same penguin in each experimental condition.

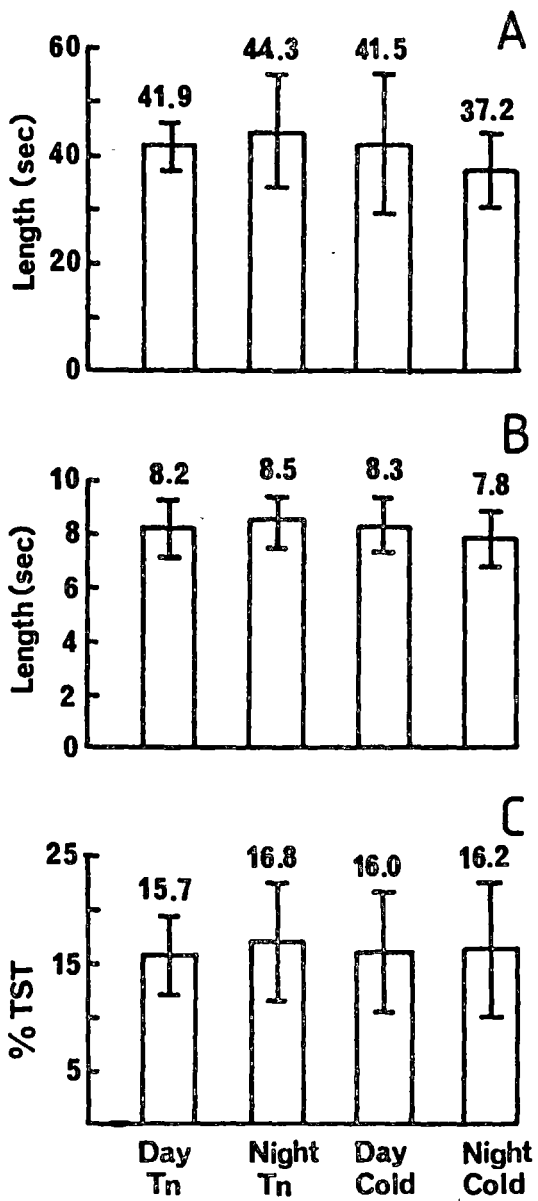

Figure 6.4 A-C. Mean sleep characteristics of little penguins at different temperatures in day and night experiments. A Length SWS (slow wave sleep) periods (s). B Length PS (paradoxical sleep) periods (s). C Relative contribution of PS to total sleep time. Standard deviations are shown by vertical lines in bar graphs.

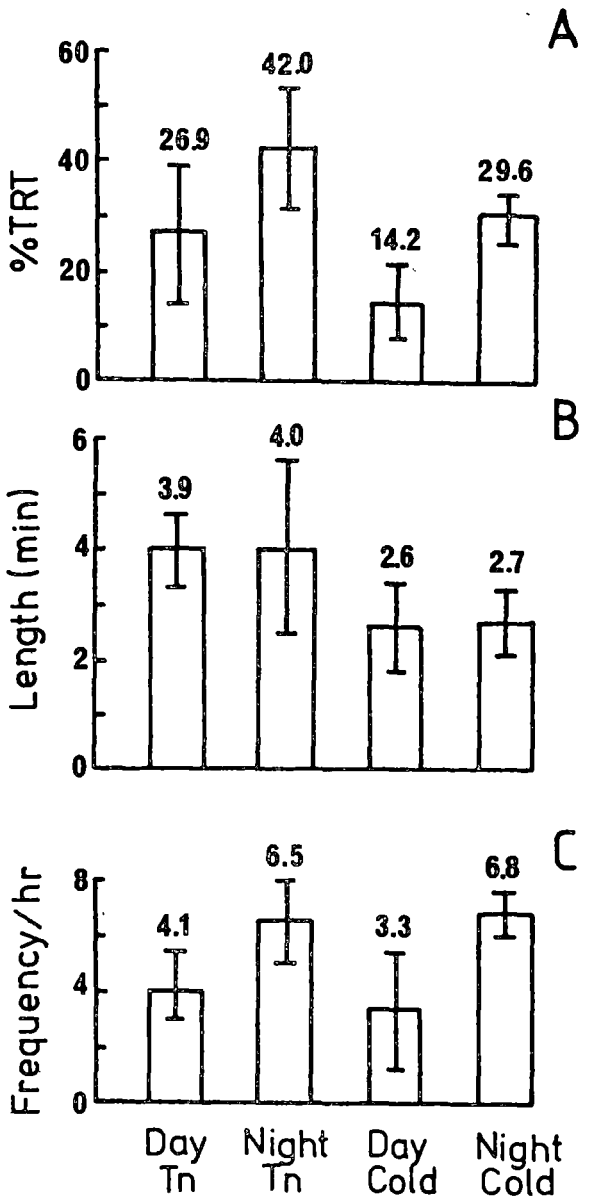

Figure 6.5 A-C. Mean characteristics of sleep in the little penguin from four hour recordings at thermoneutral and cold temperatures in day and night experiments. A Amount of sleep as percentage of total recording time. B Duration of sleep periods (min). C Frequency of sleep periods (h^{-1}. Standard deviations are shown by vertical lines. Each bar represents 8 experiments at thermoneutrality and four experiments in cold temperatures

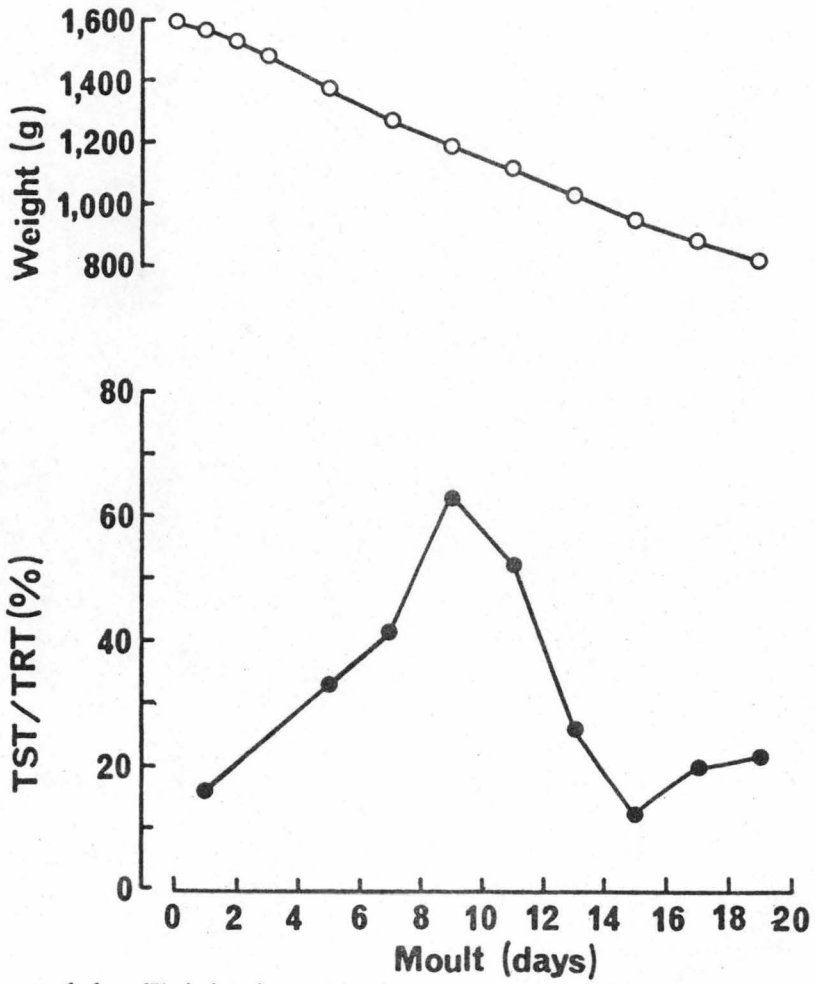

Figure 6.6. Weight loss and amount of sleep during moult in one little penguin from four hour diurnal experiments.

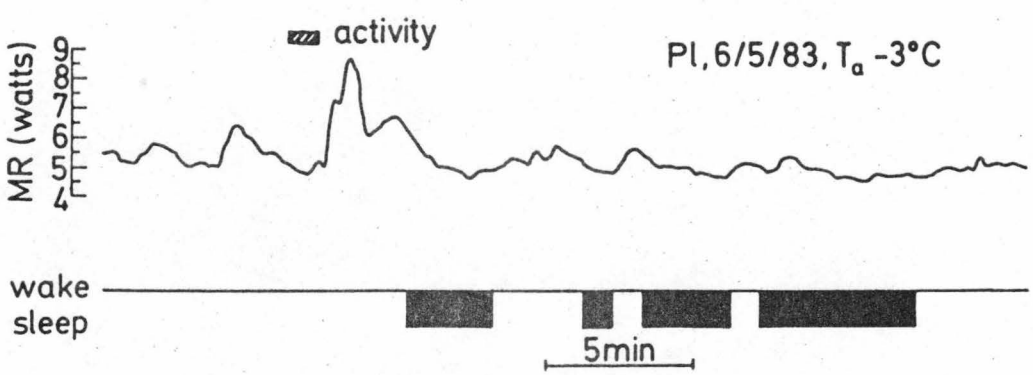

Figure 6.7. Record of metabolic rate during sleep and wakefulness in a little penguin in cold conditions. Areas shaded black represent periods of sleep. Note effects of activity upon metabolic rate.

Figure 6.4 shows the length of SWS and PS episodes in the little penguin and the contribution of SWS and PS within each sleep period. There was no significant difference between the duration of SWS and PS episodes with day and night recordings at different temperatures (Figure 6.4A,B). The mean length ($\pm$ SD) of SWS episodes from all conditions was 41.7 $\pm$ 8.60s (n=24) and the mean length of PS episodes was 8.3 $\pm$ 0.96s. The relative proportions of SWS and PS within sleep also did not significantly differ with diurnal phase and temperature. Mean percentage of PS to total sleep time from all conditions was 16.2 $\pm$ 4.74 (Figure 6.4C).

Figure 6.5 shows the amount of sleep, the duration and frequency of sleep periods of little penguins derived from four hour polygraphic recordings during day and night experiments in thermoneutral and cold conditions. Total sleep time in penguins increased at night compared with day experiments ($p < 0.005$) (Figure 6.5A). This increment of 15.1% at thermoneutrality and 15.4% in cold conditions was due to an increase in number rather than the length of sleep episodes ($p < 0.001$) (Figure 6.5C). Exposure to cold reduced total sleep time during both day and night experiments ($p < 0.025$) (Figure 6.5A). The reduction of 12.7% in day experiments and 12.4% at night was the result of a reduction in the length of sleep periods ($p < 0.025$) (Figure 6.5B).

Sleep patterns and weight loss during moult in one little penguin are shown in Figure 6.6. Food was witheld at the start of moult when the feathers on the wing lost their normal sleek appearance and the contour feathers appeared slightly ruffled. Total body weight loss was 50.75% of initial weight. Weight loss over the 19 day moult period was linear. During this period the old feathers progressively opened up until the contour feathers resembled a mosaic pattern. The first few old feathers were shed on day 7 of the moult. Feathers were first shed on the wings, then from the back and finally abdomen. Sleep patterns changed dramatically during moult. As moult progressed increased time was spent asleep until day 9 when the penguin slept for 63% of recording time. Sleep also appeared to be augmented at night as one night experiment at this time gave the time spent asleep as 75% of total recording time (TRT). Thereafter, the

TABLE 6.1
METABOLIC RATE (WATTS) OF LITTLE PENGUINS DURING SLEEP AND QUIET WAKEFULNESS AT THERMONEUTRAL AND COLD TEMPERATURES IN DAY AND NIGHT EXPERIMENTS

	Sleep[a]	Wakefulness[a]	ΔMR[b]	%Wakefulness[c]	Probability
Day, Thermoneutrality	3.87 ± 0.54	4.18 ± 0.44	-0.31	92.6	(t=3.10, n=8, p<0.02)
Night, Thermoneutrality	3.50 ± 0.48	3.74 ± 0.59	-0.24	93.6	(t=2.66, n=6, p<0.05)
Day, Cold	5.49 ± 0.90	5.89 ± 0.77	-0.40	93.2	(t=4.52, n=6, p<0.01)
Night, Cold	5.00 ± 0.76	5.54 ± 0.66	-0.54	90.3	(t=5.75, n=4, p<0.02)

a Mean ± standard deviation

b ΔMR = sleep - wake

c %Wakefulness = sleep/wakefulness x 100

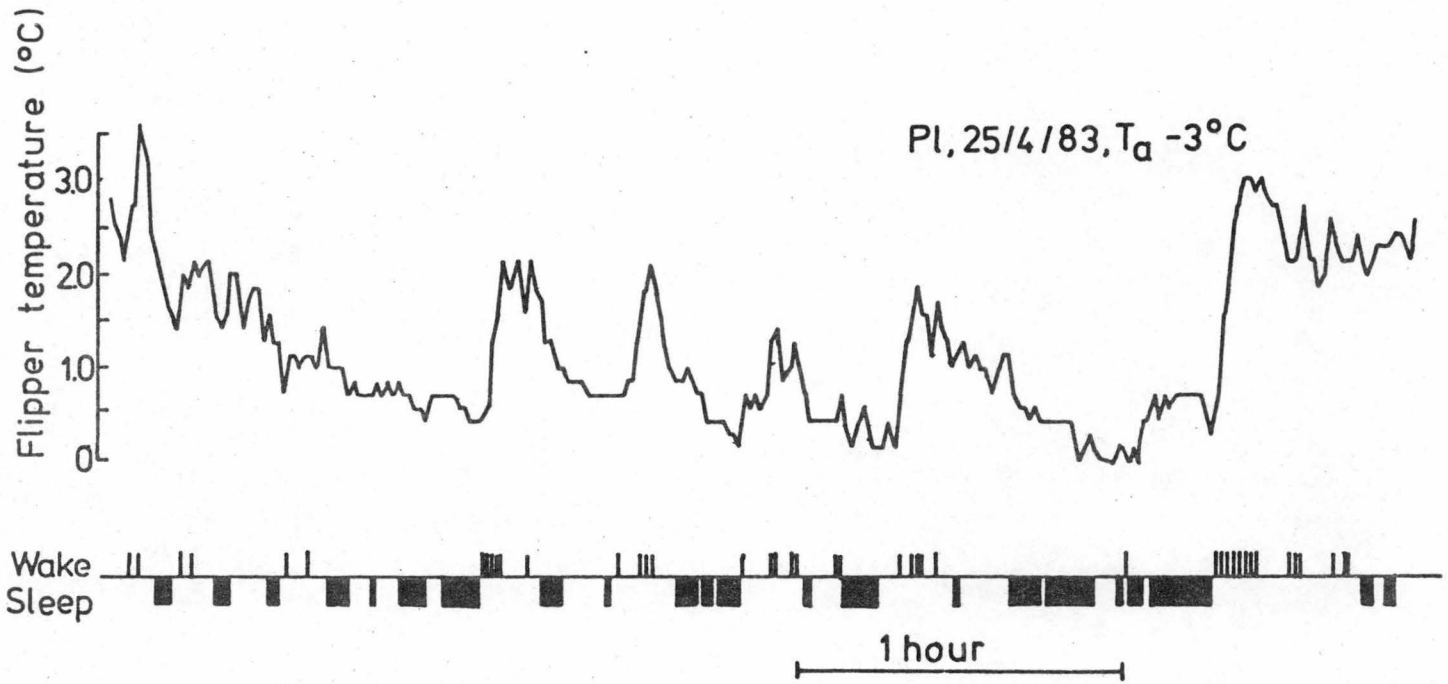

Figure 6.8. Four hour record of flipper temperature in a little penguin during sleep and wakefulness at night in cold conditions. Sleep/wake parameters scored in one minute intervals. Overall index of activity as indicated by interference in EEG records during wakefulness indicated by vertical lines for each minute observed.

amount of sleep diminished until at the end of moult, total sleep time (TST) was similar to premoult levels.

6.3.3 Metabolic Rate

Figure 6.7 shows a representative sample of metabolic rate with sleep and wakefulness in one little penguin. Metabolism varied with the amount of muscular activity but remained relatively constant during quiet wakefulness and sleep. Arousal was often associated with an increase in metabolism probably due to motor activity. The mean level of metabolism during sleep and quiet wakefulness in each experimental condition are given in Table 6.1.

Metabolic rate varied between day and night experiments. During wakefulness at thermoneutrality metabolism was 0.44 Watts lower at night than during day experiments. A similar difference of 0.35 Watts was measured between wakefulness in day and night experiments during cold exposure. In all experimental conditions, metabolic rate significantly decreased during sleep in comparison to quiet wakefulness. Metabolic rate during sleep at thermoneutrality in day and night experiments was 0.24-0.31 Watts lower than that in quiet wakefulness. At low temperatures this difference between sleep and quiet wakefulness during day and night experiments was 0.41-0.54 Watts. In both cold and thermoneutral conditions, however, there was a similar decrease of approximately 8% in metabolic rate during sleep in comparison to quiet wakefulness.

6.3.4 Temperature

A representative sample of wing temperature during sleep and wakefulness in a little penguin is shown in Figure 6.8. Most variation in wing temperature was due to muscular activity during wakefulness. Changes in peripheral temperature during sleep were simply assessed by comparing flipper temperature at the beginning and end of sleep periods greater than one minute, provided prior wakefulness also exceeded one minute. There was a mean decrease in flipper temperature of 0.15 ± 0.34°C ($t=3.4$, $n=63$, $p < 0.01$) in four experiments in cold conditions.

6.4 DISCUSSION

6.4.1 Posture and electrophysiological correlates of sleep

Sleep postures of the little penguin were similar to those seen in other penguin species, although the little penguin was never observed to sleep with the bill tucked behind one of the flippers (Boersma 1976, Murphy 1936, Spurr 1975, Van Zinderen Bakker 1971, Wilson 1907). As penguins often sleep standing upright, and even when lying down hold their heads above the ground with the beak pointing forward (Figure 6.2), it is perhaps not unexpected that muscle tone is not lost during SWS.

Polygraphic indices of sleep and wakefulness in the little penguin correspond to the general avian pattern (Goodman 1974). However, the presence of slow wave EEG activity during behavioural quiescence differed from the classic mammalian pattern of desynchronized EEG during wakefulness. These slow waves are not the result of eye movements (Figure 6.1A) and hence do not represent an artifact associated with ocular movement (Paulson 1964). Intrusion of slow waves has been reported in almost all avian polygraphic studies (section 5.4.2) and may therefore be considered typical of the avian EEG.

Slow wave activity in the avian EEG during quiet wakefulness may cause problems in defining sleep and wakefulness. Some authors have classified these periods in birds as a seperate state of vigilance as alert-resting (Ookawa 1972) or 'drowsiness (Van Twyver and Allison 1972); the latter was further defined by Van Twyver (in Chase 1972) as shown by animals which spend a lot of time awake but quiescent. Slow wave EEG activity is also observed during behavioural quiescence in a number of mammals (Rukebusch 1980) and is seperated from SWS, as in this study, by the absence of continuous slow waves. In the little penguin, no attempt was made to seperate periods of alert and quiet wakefulness in sleep analysis. Periods of quiet wakefulness were protracted and correspond to measurements of steady state metabolism, whereas alert wakefulness was often associated with activity.

6.4.2 Sleep Patterns

The proportion of PS (16.2% of TST) in the little penguin is much higher than the value normally given for birds, approximately 7% of TST (Goodman 1974). Data for the proportion of PS in mammals, however, are quite variable and range from approximately 5 to 46% of TST (Zepelin and Rechtschaffen 1974). Other avian data approach the value obtained for the little penguin. Dewasmes et al. (1984) express the contribution of PS in geese as 2.8% per 24h. Recalculation of this value in terms of the contribution of PS to total sleep time gives PS in geese as 12.2% TST. The increased amount of PS in the little penguin may be related to susceptibility to predation, one of the factors which correlates with PS patterns in mammals (Allison and Cichetti 1976). Little penguins nest in burrows and may not be as exposed as many birds, although the burrowing owl has a PS component of only 5% of TST (Berger and Walker 1972).

Although sleep parameters in this study were recorded from four-hour periods rather than from 24 h periods, it appears that sleep patterns of little penguins in this study were more evenly distributed between day and night than is evident from most avian sleep studies (Tymicz et al 1975, Walker and Berger 1972). The lower proportion of sleep at night does not appear to be due to lack of adjustment to recording conditions, since penguins also showed increased sleep time during the day when compared to the general avian pattern. A number of other birds have been characterized by polyphasic (diurnal plus nocturnal) sleep behaviour (Amlaner and Ball 1983). Although feeding at sea during the day, little penguins do not appear to be completely diurnal in their activity patterns because considerable social activity occurs at night around their burrows (Warham 1958).

King and gentoo penguins come ashore during late afternoon and return to the sea at first light (Stonehouse 1960, Van Zinderen Bakker 1971). In the continuous daylight of the antarctic summer, nesting Adelie penguins show no single period of rest but are active throughout the 24 hours (Spurr 1978). However, when not breeding or moulting many penguin species spend three to four months at a time at

sea (Stonehouse 1967). Penguins at sea may employ both nocturnal and diurnal feeding patterns, since krill (associated with squid and fish) rise to the surface at night (CR Brown, personal communication, Croxall and Prince 1980). Little penguins in southern Tasmania disperse from rookeries after breeding and moulting (Hodgson 1975). If, as seems reasonable, little penguins sleep at sea during this period then sleep patterns would probably reflect those seen in cold air temperatures rather than at thermoneutrality due to the thermal load consequent upon immersion (section 2.4.8).

The decrease in total sleep time observed with acute exposure to cold in little penguins agrees with previous mammalian research on cats (Parmeggiani and Rabini 1970) and rodents (Sakaguchi et al. 1979, Schmidek et al. 1972). By contrast, chronic exposure to cold in one ringed turtle dove resulted in an increase in total sleep time (Walker et al. 1981). The ringed turtle dove, however, exhibits shallow torpor and hence may preserve normal sleep patterns in response to cold stress, as has been found in cold exposed mammalian hibernators (Haskell et al. 1979, Walker et al. 1983).

Contrary to the mammalian pattern, in which the decrease in sleep appears to be predominantly due to a decrease in the proportion of PS, the duration of PS episodes and the ratio of PS to SWS in penguins remained relatively constant in cold compared to thermoneutral conditions. Sakaguchi et al. (1979) concluded that the decrease in PS in cold exposed kangaroo rats was the result of a decrease in the number of transitions from SWS to PS due to both altered central thermoregulatory drive and cold peripheral stimuli.

The lack of such a selective reduction in PS in the little penguin may be due to the very short duration of PS episodes. Thermoregulation is suppressed during paradoxical sleep in mammals (Heller and Glotzbach 1977, Parmeggiani 1977) and birds (Graf et al. 1981). The short duration of PS characteristic of birds suggests that there is little chance for body temperature to drift in these periods and it would not be necessary to differentially control SWS and PS in response to cold stimuli.

Cold exposure in pigeons during the dark phase of their

circadian rhythm resulted in a ratio of PS to TST of 10% (Graf et al. 1983), a value similar to the proportion of 7% of TST that pigeons spent in PS in normative sleep studies (Allison and Van Twyver 1972, Walker and Berger 1972). However, when body temperature is drastically lowered with spinal warming the proportion of PS is reduced to 0.4% of TST. Similarly, during shallow torpor in the ring necked dove, PS was successively reduced concomitant with a decrease in feathered skin temperature (Walker et al. 1981). These studies indicate that during hypothermia there does appear to be an association between peripheral cold stimuli and the amount of PS, although this would not be expressed in normal conditions.

6.4.3 Moult

The course of moult described for the little penguin is similar to other Sphenisciformes (Penney 1967) in that the feathers initially stand out and are then progressively lost as they are pushed out by new feathers growing beneath the shaft of the old. The detailed pattern of feather shedding in this study, however, differed from that given for the little penguin by Hodgson (1975) and probably simply reflects different patterns of preening. It is noticeable that the last feathers to be shed occur around the neck, an area less accessible to the beak. Groscolas (1978) pointed out that new feather growth in emperor penguins was completed by the time that feather loss began. Hence the process of feather shedding in penguins, although usually equated with moult, is primarily a mechanical process. Most physiological changes during moult would be associated with feather synthesis in the initial stages when the plumage opens up.

The increase in sleep with moult agrees with previous reports that penguins are often lethargic during moult (Penney 1967, Warham 1958). Increased sleep has also been observed in fasting geese (Le Maho, pers comm., Dewasmes et al. 1984). The decrease in sleep during the latter half of moult initially appears enigmatic. As weight loss was linear throughout moult, energy costs are inferred to be relatively constant. However, the peak in sleep time during moult approximates the division between opening of the plumage and feather shedding. The variations in TST throughout moult may then be related

to endocrine differences. In moulting emperor penguins there are peaks in plasma thyroxine and free amino acids during feather synthesis (Groscolas 1978, 1982). It is intriguing that sleep may favour protein synthesis (Adam 1980) and influence phasing of hormone release (Parker et al. 1980).

6.4.4 Metabolic Rate

Metabolic rate for little penguins during wakefulness at thermoneutrality in day experiments (3.87 Watts) were lower than presented for penguins in metabolic experiments in Chapter 2 (4.44 Watts). This may be ascribed to short sample periods and high airflow rates in this protocol although metabolic rates at thermoneutrality in wind experiments in Chapter 4 (3.75 Watts) were again lower. These values were obtained from three different groups of penguins with different experimental procedures. However, when these data were compared with each other, no significant difference was found between resting metabolic rates from each experimental condition ($F_{1,92}$= 0.92, $p < 0.5$).

The variation in metabolic rate between day and night in little penguins in this study was not simply the result of sleep. In awake birds at thermoneutrality there was still a difference in metabolism of 0.4 Watts between wakefulness during the day and wakefulness at night. Aschoff (1982) recently provided a predictive equation for the range in circadian oscillation of metabolism with weight in birds. A hypothetical one kilogram bird would be expected to decrease its resting metabolic rate at thermoneutrality by 0.7 Watts between day and night (units converted from original report), a difference almost twice that found between wakefulness during day and night in this study. If it is argued that data from birds at night in Aschoff's compilation were likely to represent sleep, then comparing the difference between wakefulness during the day and sleep at night gives a value of 0.68 Watts in the little penguin which is similar to the empirical prediction.

There have been few studies which have investigated metabolic

heat production and sleep in birds. Larochelle et al. (1982) found that black vultures sleeping with their head under a wing at relatively low air temperature (10°C) had a lower heat production than awake birds at this temperature. This difference was ascribed by the authors to postural adjustments whereby the surface area available for heat loss was reduced. At higher ambient temperatures this sleep posture would, in addition, reduce respiratory evaporative heat loss since inspired air temperature would be increased in relation to ambient and the birds would be rebreathing air of higher moisture content (Grant and Whittow 1983). In general terms, species (primarily mammalian) which have a relaxed sleeping posture would decrease metabolism as the result of a decrease in muscle postural activity from that seen in quiet wakefulness (for example Jacobsen et al. 1964). Since the sleep posture of the little penguin in these experiments was not greatly different from that seen during quiet wakefulness (Figure 6.2), it is unlikely that the decrease in metabolic rate was due to postural changes.

In addition to behavioural means of heat conservation, thermal manipulation of the hypothalamus in small mammals has shown that autonomic thermoregulatory responses decrease during sleep (Glotzbach and Heller 1976). In birds, extracerebral thermal receptors, particularly in the spinal cord, provide the dominant feedback loop for control of thermoregulation (Simon et al. 1976, see also an extensive review by Necker 1981). Cooling the spinal cord of pigeons during sleep and wakefulness revealed a decrease in the threshold for metabolic heat production during sleep (Graf et al. 1981). The present result that metabolic heat production during sleep is suppressed to an equal extent in cold and thermoneutral conditions in day and night experiments, suggests that sleep represents a constant decrease in the set point for thermoregulation.

6.4.5 Temperature

Analysis of potential temperature changes during sleep is difficult. Thermal inertia of the site of measurement (such as core temperature) and short sleep cycles in birds mask possible sleep-related temperature changes. In addition, sleep is non-homogeneous although the influence of the short PS episodes

interspersed throughout sleep in birds is likely to be minimal. Flippers and feet of penguins are important sites of sensible heat exchange (Frost et al. 1975) whereupon temperature changes during sleep should be reflected in the peripheries where there is little thermal inertia.

Flipper temperature decreased slightly in the little penguin in contrast to the increases in peripheral temperature or sensible heat loss with sleep onset noted in mammals (Haywood and Baker 1969, Roussel and Bittel 1979). However, the observed change in flipper temperature in the little penguin was of only minor importance in heat balance in comparison to the overall variation in temperature related to muscular activity during wakefulness. As such the decrease in flipper temperature may simply reflect a passive equilibration although increased peripheral temperature upon sleep onset would be maladaptive for a penguin sleeping at sea due to the large thermal heat sink represented by water (section 2.4.8). Hohtola et al. (1980) also observed that heat conservation in cold-exposed pigeons as measured by ptilomotor response was enhanced with sleep onset.

6.4.6 Energetic significance of sleep

It has been proposed that one of the major functions of sleep is to conserve energy (Allison and Van Twyver 1970, Berger 1975, Snyder 1966, Walker and Berger 1980, section 5.6.2). Evidence for this theory, however, has been mainly based on indirect arguments such as the presumed absence of sleep in ectotherms, appearance of sleep coincident with homeothermy in young animals, or correlation between sleep time and body size (Walker and Berger 1980, Zepelin and Rechtschaffen 1974).

Suppression of thermoregulatory responses during sleep can also be viewed as an energy conserving mechanism. However, there are relatively few studies which have directly investigated metabolism during sleep in comparison to quiet wakefulness. Unfortunately, many studies are variously complicated by circadian effects, and a lack of data for quiet wakefulness or activity during wakefulness (Brebbia

and Altschuler 1965, Haskell et al. 1981, Passmore and Durnin 1955, Roussel and Bittel 1979, Webb and Hiestand 1975).

The effect of sleep on nocturnal energy expenditure in sheep was examined by Toutain et al. (1977). Metabolic rate decreased by approximately 10% between sheep lying awake and during SWS. Paradoxical sleep was associated with a further but inconsequental decrease in heat production of 0-2.5% from the level observed during SWS. However, when the decrease in metabolic rate during sleep was related to total daily sleep duration, Toutain et al. concluded that the direct effect of sleep on energy expenditure was less than 2%. Passmore and Durnin (1955) suggested that sleep in fasting man is associated with a decrease of approximately 7% but also noted that this was a very small proportion of daily energy expenditure.

A similar argument can be applied in this study to the sleep related decrease in metabolic heat production and sleep time in the little penguin. A penguin would need to sleep for 24 hours to obtain a daily energy savings of 8%. Assuming a 12L:12D light cycle it can be calculated from Figure 6.5 and Table 6.1 that a resting little penguin at thermoneutrality would expend ca. 330 kJ/day. If this bird did not sleep at all, energy expenditure would increase by 2.4% compared to the normal value. Conversely, if the penguin spent all its time asleep, daily energy costs would be 4.7% less than the normal value.

Although the ubiquity of sleep implies that it provides some essential (albeit unknown) functions, this simplistic model suggests that the reduction in metabolic heat production with sleep represents only a marginal suppression in overall energy expenditure of a resting penguin at thermoneutrality. There is even less chance for sleep to conserve energy in cold conditions since total sleep time is much less than at thermoneutrality. Moreover, applying the same reasoning as above to the influence of the circadian rhythm, assuming sleep times remain unchanged but where metabolic rate is expressed for daytime values only, there would be an increase in daily energy costs of 5.3% with respect to the normal value. Theoretically, the increment in metabolic heat production upon abolition of the circadian rhythm would be approximately twice that seen with the loss

of sleep, suggesting that the circadian variation in metabolism has twice the effect of sleep in energy conservation.

It could be argued that comparison of sleep-related energetic savings in a resting bird is not strictly valid since free-living energy costs, as would be expected, are much greater that standard values (Davis et al. 1983, Kooyman et al. 1982). In these terms, the percentage of energy saved is greatly increased, although it is apparent from above that the same amount of energy could be conserved if the bird remained quietly awake during periods of inactivity rather than if it slept.

In general terms sleep-associated energy savings primarily depend upon total sleep time which must be balanced against the costs of not expending time and energy upon other variables in the energy budget. Such energy savings may be of more proximate importance in birds that spend most of the rest phase of their diurnal cycle asleep when there is little opportunity to forage. Further, during periods of enforced starvation sleep may extend limited energy reserves (Walker et al. 1981). In this context sleep is enhanced during the moult fast of the little penguin where energetic demands are met by previously stored fat reserves.

6.5 SUMMARY

The effects of sleep upon metabolic rate in the little penguin were examined at thermoneutral and low ambient temperatures in day and night experiments.

Little penguins show similar electrophysiological correlates of sleep to other birds. Sleep consists of slow wave sleep periodically interspersed with short episodes of paradoxical sleep. The amount of sleep increased at night due to increased frequency of sleep periods and decreased during cold exposure due to a reduction in the length of sleep periods.

Sleep patterns during moult in one little penguin differed greatly from non-moulting birds. Sleep time increased during the first half of moult during the period of active feather synthesis and thereafter declined to normal values.

Sleep was associated with a slight decrease of approximately 8% in metabolic rate when compared to values in quiet wakefulness in all experimental conditions. This decrease, however, represents only a marginal reduction in daily energy costs. There would be a difference of 2.4% in the hypothetical daily energy budget of a resting little penguin if it did not sleep at all. On the other hand, the increment in metabolic cost upon abolition of the circadian rhythm would be approximately twice that seen with the loss of sleep. I conclude that sleep does not normally represent an energy conserving function in little penguins.

CHAPTER 7.

CONCLUSIONS

As noted in the introduction to this thesis, penguins are extensively specialized to exploit a marine environment. This thesis attempts to explain some of the physiological adaptations and compromises to this environment that accompany the more obvious morphological differences that seperate penguins from other birds.

An aquatic lifestyle represents a severe thermal challenge to a small homeotherm due to the large capacity of water to absorb heat. As the smallest flightless marine homeotherm that spends extensive periods of time immersed at sea this thermal stress is particularly emphasized for the little penguin. The potential heat loss in water for the little penguin is two orders of magnitude greater than that in air (section 2.4.8).

Increased heat loss in water may be compensated by increased heat production although this response is energetically inefficient (section 2.4.3). Another approach is to restrict heat loss through increased insulation. Insulation in a homeotherm with fur or feathers comprises three components: environmental or boundary layer insulation, pelt or plumage insulation, and body or tissue insulation (section 4.4.3).

Environmental insulation is primarily a function of the size of the body and hence not directly amenable to selection in penguins in comparison with similar sized birds capable of flight. Plumage insulation of the little penguin is derived from a dense coat of waterproof feathers. Their waterproof function, however, has invoked a thermoregulatory paradox. Feathers achieve their insulative properties by retaining a layer of still air within their structure. Air is an excellent insulator. To achieve a waterproof function in a diving bird penguin feathers are relatively small and stiff, overlapping like tiles on a roof. Lax feathers would compress upon diving and the trapped air layer forced out whereas beyond a certain

feather length water could seep through destroying the insulation. Hence the effective depth of the penguin's feather insulation is limited and comparison of plumage thickness between penguins and other birds shows that penguin plumage is relatively shallow (section 2.4.6). As a result at low air temperatures heat transfer coefficients of penguins are comparatively high compared to other cold-exposed birds with thicker feather coats (section 2.4.5).

In partial compensation for a low plumage insulation, tissue insulation in cold-exposed penguins is extremely high (section 2.4.7). This high resistance to heat transfer was argued to primarily result from alterations in blood flow so that during cold exposure the body formed a series of cooled shells as reflected in the discrepancy between cloacal and core temperatures in the little penguin (section 2.4.1). Other birds do not appear to possess this ability. There is, however, a limit to the extent of insulation in restricting heat loss (section 2.4.8). This breakpoint was reached at a water temperature of 10°C which corresponds with the southern distribution limit of the little penguin. Below this temperature metabolic heat production increased sharply to compensate for increased heat loss.

The apparent thermal disadvantage in air conferred by the little penguin's waterproof plumage applies only to still air conditions. Upon exposure to wind and cold exposure, the rate of increase in metabolic heat production with increasing wind speed in the little penguin was much less than anticipated for a bird of similar weight (section 4.4.1). Penguin feathers in addition to withstanding water penetration provide an effective barrier to wind penetration (section 4.4.3).

The respiratory system of the little penguin is also adapted to an aquatic environment. Ventilation must be adjusted to the demands of respiratory gas exchange and thermoregulation. The little penguin's diving lifestyle has resulted in a slow resting respiratory cycle with a very high oxygen extraction efficiency from inspired air (sections 3.4.2, 3.4.3). This pattern of gas exchange allows rapid replenishment of blood oxygen stores between dives but appears to have also resulted in an inability to invoke a typical avian panting response with heat exposure (section 3.4.3). Other work has shown

respiratory evaporative heat loss remains low and disruption of the acid-base status limits the little penguin's tolerance to heat.

The thermoregulatory and energetic consequences of changes in the external environment such as wind and water are readily apparent. Changes in the internal environment, such as sleep however, are less clear. Sleep is ubiquitous among all birds and mammals although its importance and physiological mechanisms are not well understood (sections 5.6, 5.7). Of potential importance in comparative studies of thermoregulation and energetics is the hypothesis that sleep represents a substantial saving of energy (section 5.6.3).

Little penguins were classified as having polyphasic sleep patterns with sleep being more evenly distributed between day and night than in most birds which correlates with the unusual activity cycle of the little penguin (section 6.4.2). Sleep in little penguins resulted in a slight decline in metabolic rate associated with a decrease in the setpoint for body temperature regulation (section 6.4.4). This change in body temperature set-point with sleep is common to all birds and mammals so far studied and limits the amount of sleep at low ambient temperatures. The decline in metabolic rate with sleep, however, has rarely been studied and represents only a small percentage of daily energetic costs (section 6.4.6). Sleep cannot hence be regarded as an energy conserving mechanism in the little penguin. A polyphasic sleep pattern may have resulted in a much smaller circadian difference in metabolic rate between day and night than that found in most birds.

These results show that physiological parameters of the little penguin differ substantially from general avian patterns and may be explained by reference to their adaptive significance in exploiting a marine environment. Such physiological adaptations, however, have often resulted in a compromise between environmental demands and constraints imposed by the little penguin's avian lineage.

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APPENDIX 1. EXTANT PENGUIN SPECIES

SPECIES	COMMON NAME
Aptenodytes forsteri	Emperor penguin
A. patagonica	King penguin
Megadyptes antipodes	Yellow-eyed penguin
Pygoscelis adeliae	Adélie penguin
P. antarctica	Chinstrap penguin
P. papua	Gentoo penguin
Eudyptes chrysolophus	Macaroni penguin
E. schlegeli	Royal penguin
E. atratus (sclateri)	Erect-Crested penguin
E. crestatus (chrysocome)	Rockhopper penguin
E. pachyrhynchus	Fiordland penguin
E. robustus	Snares Island Penguin
Spheniscus mendiculus	Galapagos penguin
S. humboldti	Peruvian penguin
S. magellanicus	Magellanic penguin
S. demersus	Jackass penguin
Eudyptula minor	Little penguin
E. m. iredalei	Chatham Island Penguin
E. albosignata	White-flippered penguin

APPENDIX 2. PENGUIN MAINTENANCE

Little penguins used in these studies were caught at Marion Bay, 50 km East of Hobart and maintained in a covered outdoor enclosure provided with nesting boxes and a pool of fresh water.

Although initially forcefed after capture, the penguins quickly adapted to being handfed on a diet of salmon supplemented by multi-vitamins and calcium. The amount of food was adjusted according to the birds' demands. Further supplements of sulphur-containing amino acids (Cysteine, Methionine) were provided prior to moult to meet the potential demands for keratin synthesis.

Each group of penguins was held in captivity for approximately one year and released at the capture site on completion of experiments.

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APPENDIX 3. PUBLISHED WORK

Temperature regulation in the little penguin, Eudyptula minor, in air and water.

Sleep and metabolic rate in the little penguin, Eudyptula minor.

Stahel, CD & Nicol, SC, 1982, Temperature regulation in the little penguin, Eudyptula minor, in air and water. Journal of comparative physiology. B, Biochemical, systemic, and environmental physiology 148:93-100

Stahel, CD; Megirian, D & Nicol, SC, 1984, Sleep and metabolic rate in the little penguin, Eudyptula minor, Journal of comparative physiology. B, Biochemical, systemic, and environmental physiology 154:487-949